SILURIAN ENCRINURID TRILOBITES FROM GOTLAND AND DALARNA, SWEDEN

by LARS RAMSKÖLD

ABSTRACT. Trilobites of the family Encrinuridae are described from the Silurian of Gotland and Dalarna, Sweden. Twelve species (nine named, of which four are new) are assigned to two genera. Three subgenera of *Encrinurus* are recognized, including *E.* (*Australurus*) subgen. nov. and *E.* (*Nucleurus*) subgen. nov. *Balizoma* is redefined by excluding species here included in *E.* (*Nucleurus*). A directional, morphological trend is shown between several populations of *E.* (*Encrinurus*) *macrourus* Schmidt, 1859. *E.* (*E.*) *schmidti* Männil, 1968 is a junior subjective synonym of *E.* (*E.*) *schisticola* Törnquist, 1884. *Balizoma obtusus* (Angelin, 1851) may be a widespread species, possibly occurring also in Britain, Estonia, Czechoslovakia, Podolia, and Canada. New species described are *E.* (*E.*) *intersitus*, *E.* (*E.*) *jarkanderi*, *E.* (*E.*) *nasutus*, and *E.* (*E.*) *odvaldensis*.

ONE of the earliest records of a trilobite from Sweden is Linnaeus' (1759) figure and description of a pygidium of *Encrinurus*, in all probability from Gotland, that he included under the general name *Entomolithus paradoxus*. Nearly sixty years later Wahlenberg (1818) erected the species *Entomostracites punctatus*, which has since become one of the most commonly cited Silurian trilobite species. Other Swedish Silurian encrinurids were described subsequently by Angelin (1851), Schmidt (1859), and Törnquist (1884). More recently Tripp (1962) revised some species of *Encrinurus* from Gotland. Encrinurids in general have received considerable attention lately, with several important works on taxonomy, morphology, and phylogeny (Evitt and Tripp 1977; Temple and Tripp 1979; Strusz 1980).

This paper is a study of Silurian encrinurids from Gotland and Dalarna. Two additional species from Gotland are being described by C. Magnus (Bergen, Norway), and a further species from the Llandovery of Östergötland is currently being studied (Ramsköld and Bassett, in prep.). During the course of this work it became necessary to study all descriptions of Silurian encrinurids, and to examine the major British and Australian collections of encrinurids. This has led to the recognition of three subgenera of *Encrinurus* and a re-evaluation of *Balizoma*, with bearings on other encrinurine genera.

The stratigraphical scheme used for the Gotland sequence (text-fig. 1) is that of Hede (1921, 1925); subunits are those of Laufeld (1974*a*). Hemse Marl, northwestern part, and Hemse Marl, southeastern part are abbreviated Hemse Marl NW and Hemse Marl SE, respectively. It must be emphasized that the stratigraphical distribution of the species as plotted in text-fig. 1 does not necessarily reflect the chronological succession of the taxa, due to diachroneity of most units. The stratigraphical terms for Dalarna follow Waern (1960).

NOTES ON MORPHOLOGY

General terminology. The terminology used here mainly follows the *Treatise on Invertebrate Paleontology*, and Evitt and Tripp (1977). The terms '4L' and 'PL' were defined by Howells (1982) and 'eye socle' by Shaw and Ormiston (1964). Following Tripp *et al.* (1977) the term 'tubercle' is used in its conventional general sense rather than *sensu* Miller (1976) since a precise distinction requires thin sections. 'Rachis' and 'rachial furrow' are preferred to the slightly misleading 'axis' and 'axial furrow', as is 'labral plate' to the anatomically incorrect 'hypostome'. Use of the terms 'anteromedian depression', 'sagittal band', and 'sagittal groove' follow Strusz (1980). Temple and Tripp (1979)

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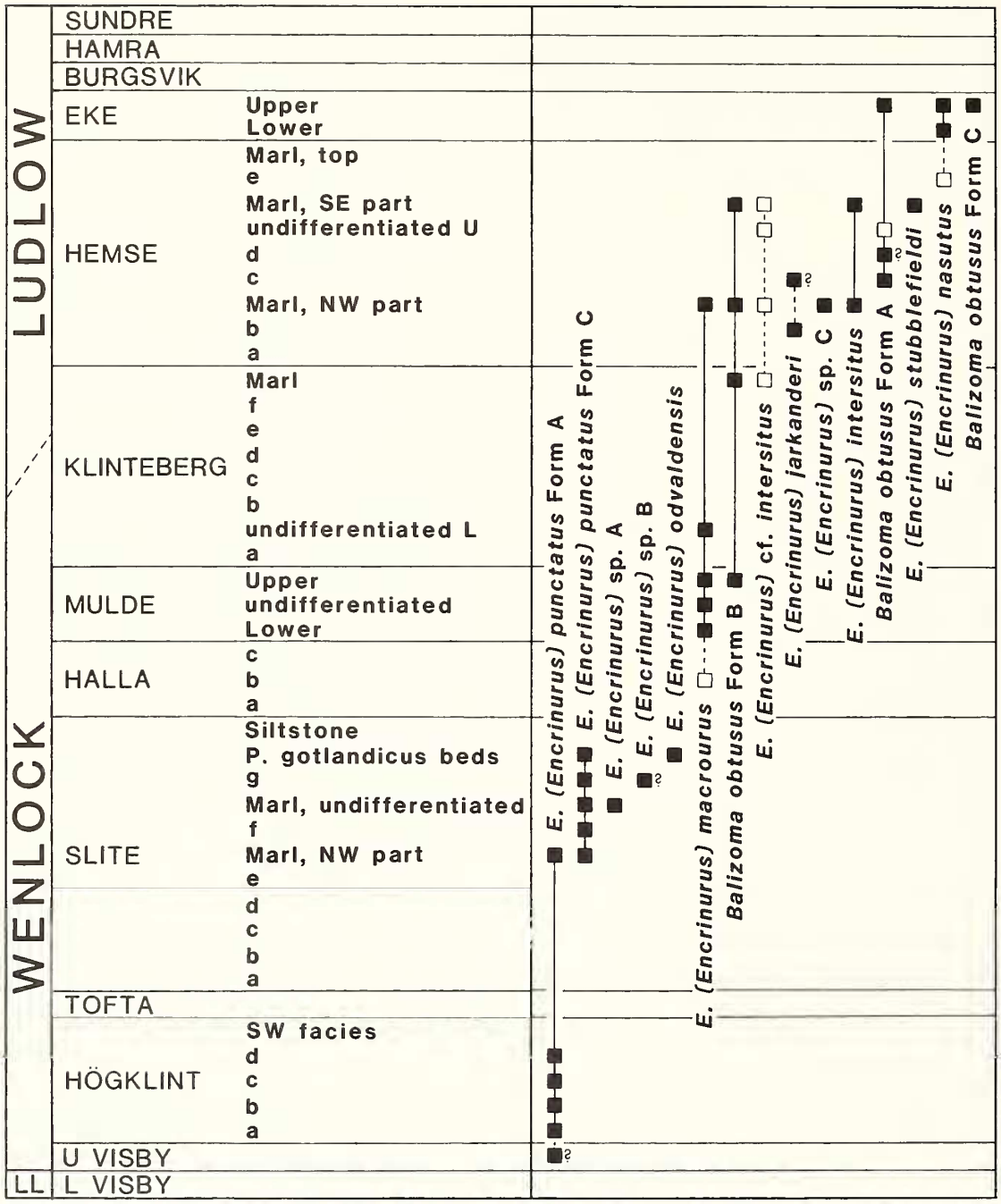
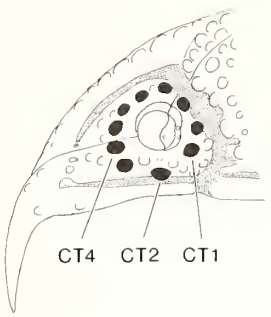


TEXT-FIG. 1. Occurrence of Encrinuridae in Gotland. Solid squares represent specimens assigned definitely to a taxon and open squares represent compared forms. A square with a question mark indicates that the horizon is uncertain. The stratigraphical column is a practical way of illustrating the distribution of the species within the mapped units, but is not necessarily a reflection of the chronological appearance and disappearance of various taxa. Diagram modified from Laufeld (1974*a*, p. 124).



TEXT-FIG. 2. The circumocular tubercles CT1–CT4. Tubercle CT3 is sometimes double, or displaced posterolaterally, and has not been used in the measurements (Table 1). Drawing based mainly on *Encrinurus* (*Encrinurus*) *punctatus* Form A (Ar51797).

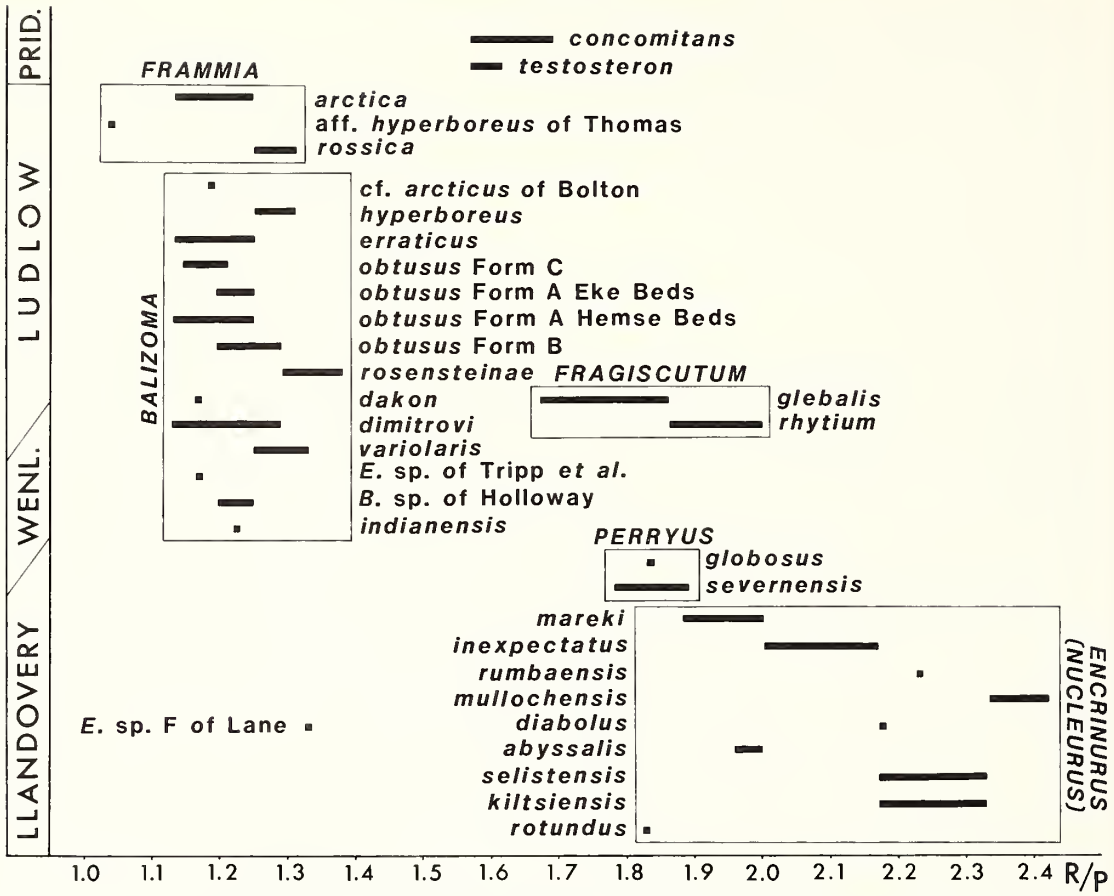
redefined several other terms as a basis for their attribute list, and these are adopted here. The mucro is taken as beginning where the curved slope posterior to the end of rachis meets the flat (in lateral view) surface of the most posterior pygidial part. Certain important features of encrinurid morphology are discussed in some detail below.

1. *Glabellar tubercle formula.* A row of six tubercle-pairs along the glabellar mid-line is already present in the Middle Ordovician *Encrinuroides neuter* and *E. uncatus* described by Evitt and Tripp (1977). The gross morphology of these species suggests a position close to the ancestry of *Encrinurus s.l.* This basal tubercle pattern is retained in *E.* (*Encrinurus*) and *E.* (*Nucleurus*), and is present, though less clear, in the later offshoots *Balizoma* and *Frammia.* The pattern is obliterated or lost in *E.* (*Australurus*). In *Encrinurus* much taxonomic emphasis has been placed on the arrangement of the glabellar tubercles, as expressed in the system elaborated by Tripp (1957, 1962) and further refined by Strusz (1980). The Gotland material (and British; P. D. Lane, pers. comm.) shows that the detailed pattern is different at almost every locality, and that most of these small differences cannot be of importance at levels above populations or subspecies. For this reason complete tubercle formulae are of limited use and are not included in the diagnoses of the species described here, although particular tubercles may be of diagnostic importance.

2. *Circumocular tubercles.* In *E.* (*E.*) *punctatus* and allied species the eye socle is surrounded by a more or less distinct ring of prominent tubercles. On the fixed cheek four major tubercles, here called CT1–CT4 (see text-fig. 2), form part of the circle, usually together with several additional minor tubercles. CT1 is the torular tubercle and CT2 the postocular tubercle of Evitt and Tripp (1977). The relative positions of CT1–CT4 and the distinctness of the part of the circle on the free cheek are useful diagnostic features. The ring itself probably had little functional significance, being partly at least an expression of density of general tuberculation rather than of a particular function of the tubercles surrounding the eye. Individual tubercles, however, may have had a specialized function (cf. torular tubercle in Evitt and Tripp, 1977).

3. *Main tubercle row on free cheek border.* In all species of *E.* (*Encrinurus*) there is a row of prominent tubercles on the free cheek border along the lateral border furrow. Anteriorly there is a commonly smaller tubercle further from the lateral border furrow, close to the anterior furrow. This is followed by a row of six large tubercles close to the border furrow, and a posterior, smaller tubercle set further from the border furrow. Posterior to this tubercle, and closer to the border furrow, there begins a row of four to six tubercles along the sutural edge of the free cheek border; these tubercles are progressively smaller posteriorly. This tubercle arrangement is consistent throughout the subgenus, but may be subdued and almost lost, as in *E.* (*E.*) *stubblefieldi.* A similar, but less regular tubercle pattern is already present in *Encrinuroides neuter* and *E. uncatus*, and also in *Balizoma.* In *Encrinurus* (*Encrinurus*) the expression of the main tubercle row is a useful diagnostic criterion.

4. *R/P ratio in the pygidium.* R = number of rachial rings anterior to the intersection (as defined by Temple and Tripp 1979, fig. 3) of the last, not distally converging, pair of pleural furrows and the rachial furrows. P = number of pleural ribs anterior to the same pair of pleural furrows. The



TEXT-FIG. 3. R/P ratios for certain encrinurids. The species are arranged approximately chronologically, but there are probably several errors due to poor data. Each supraspecific taxon has a limited range of the R/P ratio and a restricted vertical distribution. Authorships of the species are given in the discussions of *Balizoma* and *Encrinurus* (*Nucleurus*).

R/P ratio defines the spacing of the rachial rings relative to the pleural ribs. The ratio eliminates the problem of making accurate counts of the often indistinct posteriormost rings. R/P ratios are very stable in encrinurid genera and may therefore aid in supraspecific grouping. They are easy to calculate, not influenced by distortion, identical on internal and external moulds, and confined to the most commonly preserved part of the exoskeleton. An R/P ratio analysis for particular encrinurid species is given in text-fig. 3.

5. *Terminal rib notation.* A numbering system is used here for the terminal pleural ribs. Counting from the anterior rib, the number of the last rib (N) is given, and a coefficient indicates whether this rib is paired (N^2) or single (N^1; it may be ridge- or knob-shaped). The number of pleural ribs is not dependent significantly on pygidial size (Howells 1982, text-fig. 4; text-fig. 8 herein), although there may sometimes be a tendency for more ribs in large specimens. The system can be used for all encrinurids, but is best suited for non-mucronate forms.

6. *Axial tubercles* are a conspicuous feature in many encrinurid pygidia and were mentioned and figured as early as 1759 by Linnaeus. The positions of such tubercles were studied by Norton (1895), and Rosenstein's (1941) detailed work showed the strict regularity of the tubercle distribution in Estonian material. In Best's (1961) comprehensive study of a large collection, tubercle distribution

patterns were interpreted as indicating a response to changing environmental conditions, though Perry and Chatterton (1979) preferred a hypothesis of immigrating races. It is now common to include a modal distribution pattern for these tubercles in descriptions when possible (Campbell 1967; Männil 1978; Šnajdr 1978; Perry and Chatterton 1979). More extensive information has sometimes been added (Männil 1968; Tripp *et al.* 1977; Howells 1982) and a detailed notation system has been elaborated (Strusz 1980). From these studies it is clear that the number of blank rachial rings between those bearing tubercles is fairly constant in each species, and that the entire 'set' of tubercles often has two or more alternative positions along the sagittal line. As a somewhat simplified comment, *Balizoma* has a tubercle on every second ring, *Fragiscutum* and *E.* (*Nucleurus*) on every third, and *E.* (*Encrinurus*) on every fourth. This tubercle distribution obviously correlates strongly with the number of rachial rings and, in turn, with the R/P ratio. A pygidium with numerous, short (sag.) rings (= high R/P ratio) will have several blank rings between the tubercle-bearing rings to allow an inter-tubercle distance comparable to that of a pygidium with few, long rings (= low R/P ratio), where less than every second ring is blank. This correlation between distance and position of the tubercles seems to indicate a functional significance of the tubercle arrangement. However, it also means that the taxonomic value of the modal distribution may be limited, since the arrangement reflects dependence on these functional requirements (i.e. a certain distance between the tubercles) rather than an obligate interrelationship between a tubercle and a particular ring. It is likely that the tubercle distribution, as expressed in ring positions, is controlled to a large extent by the number of rachial rings (which depends on the sagittal length of the rings), and that this latter feature is of more primary taxonomic importance.

SYSTEMATIC PALAEONTOLOGY

The specimens are housed in Naturhistoriska Riksmuséet, Stockholm (prefixed Ar), in the Type Collection of the Geological Survey of Sweden (SGU), and in the Palaeontological Institute, University of Lund (LO). All specimens, except in SEM photos, were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. Terms for the orientations used during photography follow Whittington and Evitt (1954, p. 11) Most specimens with numbers beginning Ar51 and Ar52 were collected by the author; other collectors are indicated in the plate explanations when known.

Family ENCRINURIDAE Angelin, 1854

Diagnosis. See Strusz 1980, p. 7.

Subfamily ENCRINURINAE Angelin, 1854

Diagnosis. See Strusz 1980, p. 7.

Discussion. The origin of the encrinurids discussed in this study is somewhere near the American Trentonian *Encrinuroides neuter* and *E. uncatus* described by Evitt and Tripp (1977). No certain descendant species are as yet known from the uppermost Ordovician. This apparently small group underwent prolific radiation in the lower and middle Llandovery as three main lineages (the *variolaris*, *punctatus*, and *mitchelli* plexa of Strusz 1980). These lineages are regarded as constituting the genus *Encrinurus*, and are here given subgeneric status. Two of these subgenera, *E.* (*Encrinurus*) (= '*punctatus*') and *E.* (*Australurus*) (= '*mitchelli*'), remained relatively stable through the Silurian while one, *E.* (*Nucleurus*) (= '*variolaris*'), proliferated further and gave rise to *Balizoma*, *Fragiscutum*, and *Frammia*.

Genus ENCRINURUS Emmrich, 1844

Type species. Entomostracites punctatus Wahlenberg, 1818 (ICZN Opinion 537, 1959, emended 1977), from the Högklint and Slite Beds (Wenlock) of Gotland, Sweden.

Other species. A list of assigned species is given under each of the three subgenera recognized here. A few additional species apparently belong to *Encrinurus*, but are too poorly known to be assigned to any particular subgenus. These are: *E. calgach* Lamont, 1948; *E. creber* Maksimova, 1962; *E. donenjalensis* Balashova, 1968*b*; *E. dris* (Lamont, 1948); *E. henshawensis* (Lamont, 1978); *E. laosensis* Patte, 1929; *E. marianne* Maksimova, 1975; *E. penkillensis* (Lamont, 1978); *E. ploeckensis* von Gaertner, 1930*a*; *E. shelvensis* Whittard, 1938; and possibly *E. nodai* Kobayashi and Hamada 1974.

A distinct group is formed by three late Llandovery species; the American *E. americanus* Vogdes, 1886, and the two Estonian *E. pilistverensis* Rosenstein, 1941 and *E. quinquecostatus* Männil, 1958. Only the pygidia are known of these species, but they are so different from other encrinurids that they will certainly form a new genus when better known.

A few species included by Strusz (1980) in *Encrinurus* are regarded here as being outside the range of this genus (though reassignments are outside the scope of this study): *Encrinuroides meijiangensis* Chang, 1974; *E. meitanensis* Chang, 1974; *Encrinurus melzensis* Krueger, 1971; *E. rialpensis* von Gaertner, 1930*b*; *E. simplicicuhus* Talent, 1965. *E.? newlandensis* (Lamont, 1978) of Howells (1982) does not belong to *Encrinurus*.

Diagnosis. Glabella with regular and more or less coarse tuberculation and short (tr.) lateral glabellar furrows not deeply impressed across glabella. Preglabellar furrow faint to obscure axially. 2L–4L and PL tuberculiform, 1L may be considerably reduced. Glabellar lobes and tubercles on fixed cheek along rachial furrow equal in number, set in alternating or opposing positions. Anterior cranidial border widening abaxially, with one row of tubercles. Eyes pedunculate or stalked, opposite 2L to 3L. Rhynchos ends only slightly posterior to labral suture or protrudes beyond this. Pygidium subtriangular, at least eight pleurae and fourteen rachial rings; axial tubercles and sagittal band or groove present, may be faint.

Remarks. Strusz's (1980) diagnosis has been slightly amended, mainly to adjust for the exclusion of species since included in *Balizoma*.

Subgenus ENCRINURUS (ENCRINURUS) Emmrich, 1844

Type species. As for genus.

Other species. *E. balticus* Männil, 1978; *E. caplanensis* Northrop, 1939; *E. confusevarus* Howells, 1982; *E. deomenos* Tripp, 1962; *E. egani* Miller, 1880; *E. expansus* Haswell, 1865; *E. hagshawensis* Lamont, 1965; *E. intersitus* sp. nov.; *E. jarkanderi* sp. nov.; *Cryptonymus laevis* Angelin, 1851; *E. macrourus* Schmidt, 1859; *E. nasutus* sp. nov.; *E. odvaldensis* sp. nov.; *E. onniensis* Whittard, 1938; *E. ornatus* Hall and Whitfield, 1875; *Zethus pagei* Haswell, 1865; *E. reflexus* Raymond, 1916; *E. ruhnnensis* Männil, 1978; *E. schisticola* Törnquist, 1884 (including the junior subjective synonym *E. schmidti* Mannil, 1968); *E. stateratus* Howells, 1982; *E. stubblefieldi* Tripp, 1962; *E. triangulus* Männil, 1977; *Asaphus tuberculatus* Buckland, 1836. Two more species, *E. brevispinosus* Haas, 1968 and *E. squarrosus* Howells, 1982, differ in detail from the above species, and can only be assigned questionably to the nominate subgenus.

Diagnosis. Glabella relatively long and narrow. Anterior border of cranidium with eight to fourteen tubercles, usually eight to ten. Tubercles on fixed cheek along rachial furrow equal in size to

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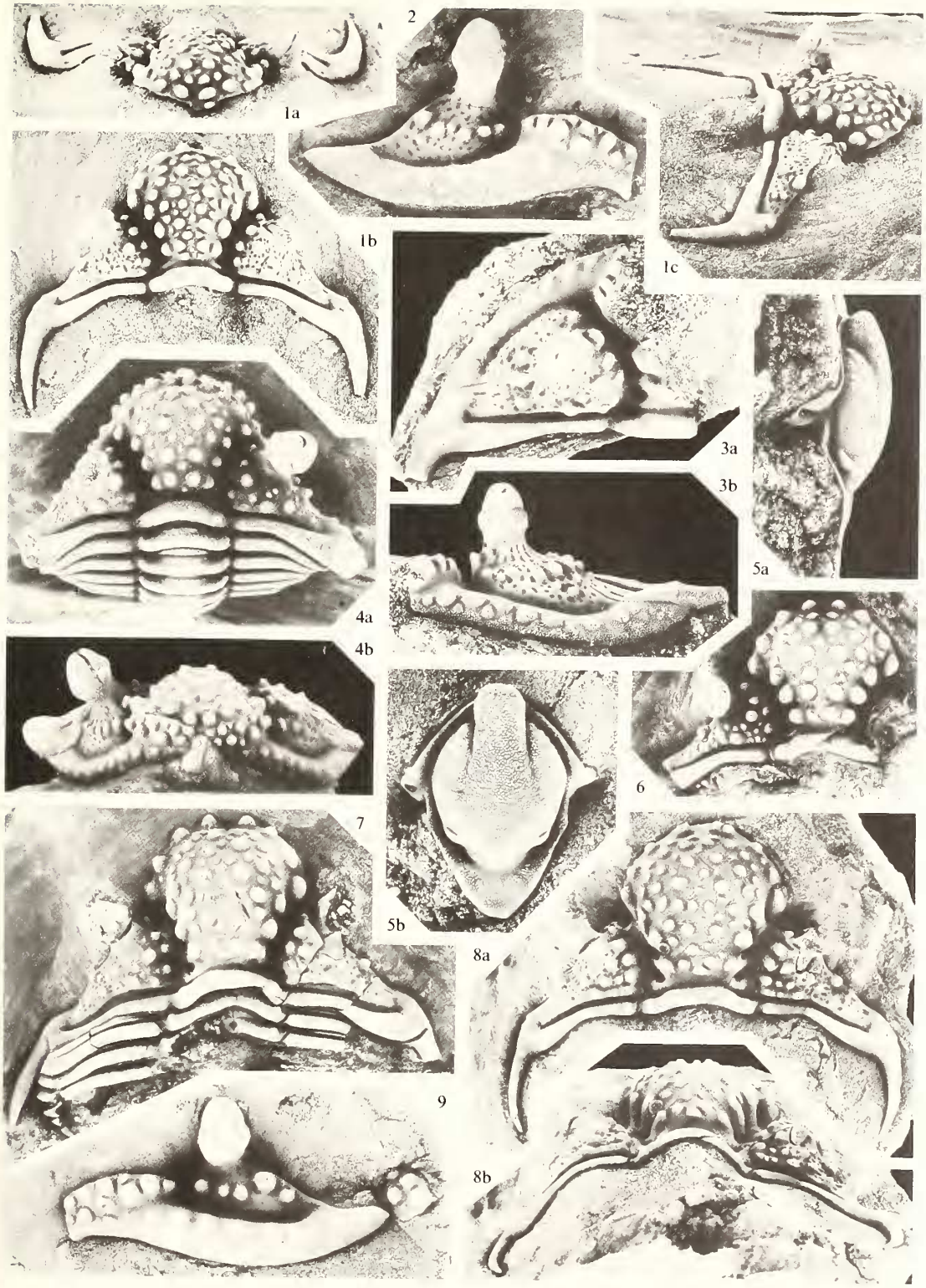
EXPLANATION OF PLATE 37

Figs. 1–9. *Encrinurus* (*Encrinurus*) *punctatus* (Wahlenberg, 1818), Form A. Högklint Beds, unit a (1, 5, 7, 8), unit b (2–4), Slite Beds, Slite Marl (6, 9). Ireviken 1 (1, 5), Kopparsvik (8), Lickershamn (3, 7), Valve 2 (6, 9), Vattenfallsprofilen 1, 19·90–20·25 m a.s.l. (2, 4). 1*a–c*, Ar51784, anterior, dorsal, and oblique lateral views of cranidium, × 3. 2, SGU 5045, exterior view of free cheek, × 4 (coll. G. Liljevall 1908). 3*a*, *b*, Ar51797, views normal and parallel to length axis of eye of incomplete cephalon, note circumocular tubercles, × 3 (coll. Amelang 1978). 4*a*, *b*, Ar49774, dorsal and anterior views of enrolled specimen, × 3 (coll. V. Jaanusson 1975), 5*a*, *b*, Ar51785, lateral and exterior views of labral plate, × 6. 6, Ar52293, dorsal view of incomplete cranidium, × 2. 7, Ar52288, dorsal view of cranidium with part of thorax, × 2 (coll. U. Samuelson 1984). 8*a*, *b*, Ar52287, dorsal and posterior views of cranidium, × 2. 9, Ar52294, exterior view of free cheek, × 3.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *punctatus*

other fixed cheek tubercles. 1L small, ridge-shaped, set well below 2L, occasionally tuberculiform abaxially. Genal angle usually with long spine, sometimes short, rarely almost lost in adults. Labral plate with wide rhynchos, level with or protruding in front of labral suture, posterior border 19–23 % of labral length. Thorax commonly with axial spine on tenth segment. Pygidium fairly long and narrow, mucronate; mucro formed by eighth and following pleural segments. Usually 8^2–9^1 pleural pairs, posterior pleurae not merging into 'loop'.

Remarks. The great majority of species referred to this subgenus are characterized by their spinosity (genal and thoracic spine and mucro). The earliest species (?lower–middle Llandovery) are less spinose and show considerable similarities to *E.* (*Nucleurus*) subgen. nov., probably indicating that these two lineages split near the Ordovician/Silurian boundary. The number of free pleurae in the pygidium was already fixed by middle Llandovery times, being seven in all assigned species. *E. squarrosus* from the lower Llandovery of Scotland is assigned only questionably to *E.* (*Encrinurus*) since it, together with other differences, has a variable number of free pleurae and practically no mucro; this may indicate the condition before the number of free pleurae was fixed. A small group of upper Llandovery-lower Wenlock species (*E. laevis*, *E. triangulus*, and an undescribed Gotland species) differ from the main line by the reduced genal spines, subdued tuberculation on the free cheek, low eyes, and low R/P ratio ($< 2{\cdot}0$ as opposed to 2·3–3·0 for most *E* (*E.*) species). They are not, however, sufficiently different to form a separate subgenus as presently known.

Encrinurus (*Encrinurus*) *punctatus* (Wahlenberg, 1818)

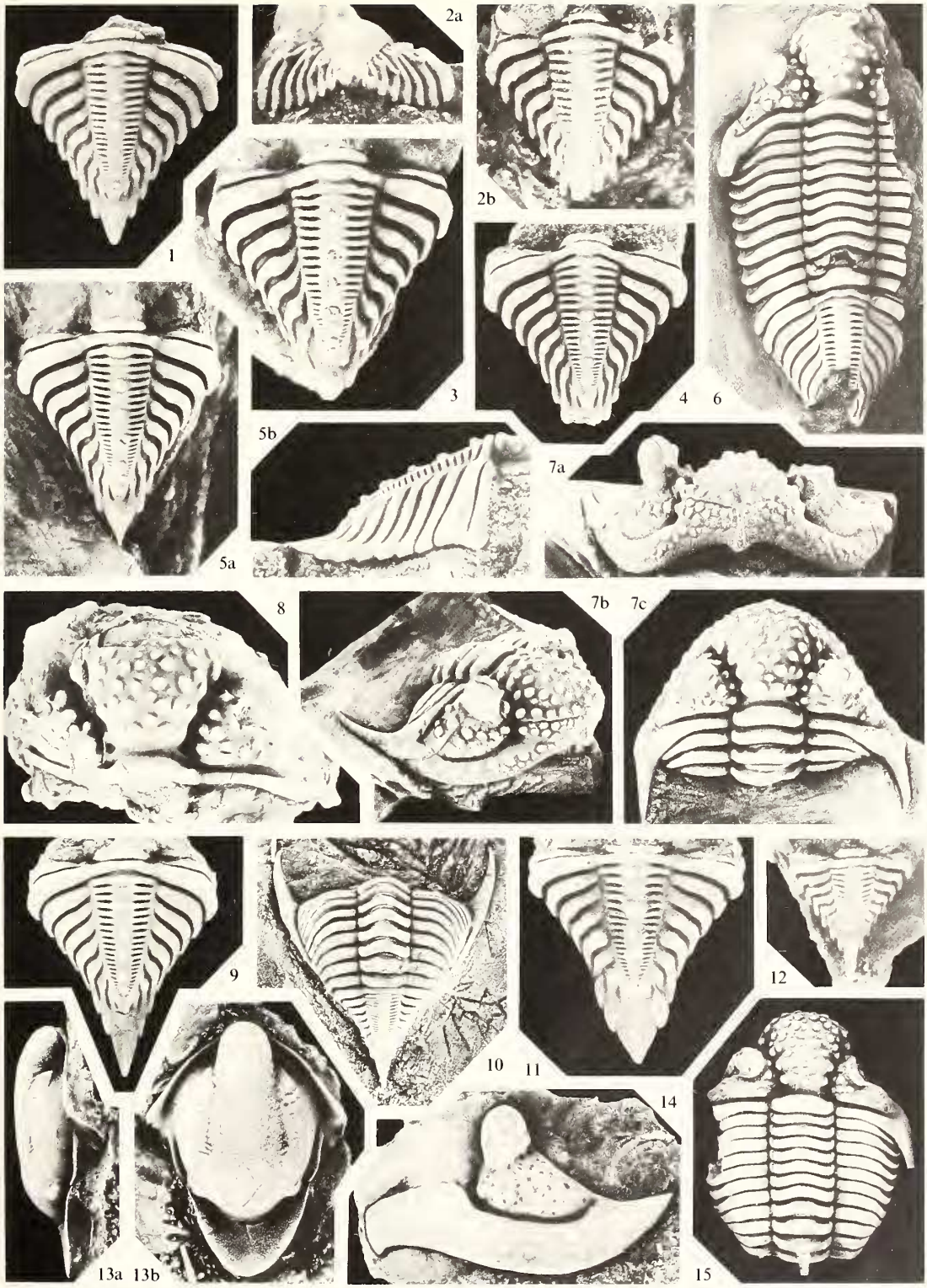
Plate 37, figs. 1–9; Plate 38, figs. 1–15

v* 1818 *Entomostracites punctatus* Wahlenberg, p. 32, pl. 2, fig. 1* [*non* fig. 1].
v. 1827 *Calymene punctata*; Dalman, p. 233 (48), pl. 2, fig. 2*a*, *b*.
v. 1837 *Calymene punctata*; Hisinger, p. 12, pl. 1, fig. 9 [copy Dalman 1827, pl. 2, fig. 2*a*].
? 1847 *Encrinurus punctatus* Wahlenb.; Hawle and Corda, p. 91, pl. 5, fig. 55 [Gotland specimen].
? 1851 *Cryptonymus punctatus* Wahl.; Angelin, p. 3, pl. 4, figs. 4–8.
v. 1901 *Encrinurus punctatus* Wahlenberg; Lindström, p. 56, pl. 4, figs. 4–9, 12, 13.
. 1941 *Encrinurus punctatus* (Wahlenberg) 1821; Rosenstein, p. 53, pl. 1, figs. 1–11 [*non* pl. 2, fig. 4 = *E.* (*E.*) *macrourus* Schmidt, 1859]. [With synonymy list.]
? 1954 *Encrinurus punctatus* (Wahlenberg) 1821; Balashova, p. 41, pl. 24, figs. 7–9.
v. 1956 *Encrinurus punctatus* (Wahlenberg, 1821); Tripp and Whittard, p. 259, pl. 3, figs. 1 and 2.
v. 1962 *Encrinurus punctatus* (Wahlenberg); Tripp, p. 461, pl. 65, figs. 9–11, 13, 14; pl. 66, figs. 2 and 3; pl. 67, figs. 5–8; pl. 68, figs. 7, ?8, 10.
v. 1962 *Encrinurus macrourus* Schmidt; Tripp, p. 469, pl. 65, fig. 2 only.
v. 1962 *Encrinurus tuberculatus* (Buckland); Tripp, p. 467, pl. 65, figs. 5–8; pl. 66, figs. 4–6, 8–11 [*non* fig. 7]; pl. 67, figs. ?9 and ?10; pl. 68, fig. 4 [*non* figs. 5 and 6]. [With synonymy list.]

EXPLANATION OF PLATE 38

Figs. 1–5. *Encrinurus* (*Encrinurus*) *punctatus* (Wahlenberg, 1818), Form A. All Högklint Beds, unit a. Halls Huk 1 (2), Ireviken 1 (3–5), Kopparsvik (1). 1, Ar52285, dorsal view of pygidium, ×6. 2*a*, *b*, Ar52289, posterior and dorsal views of small pygidium, ×11. 3, Ar52283, dorsal view of strongly tuberculated pygidium, ×4. 4. Ar52284, dorsal view of pygidium, ×4. 5*a*, *b*, Ar52282, dorsal and lateral views of pygidium, ×4.

Figs. 6–15. *E.* (*E.*) *punctatus* (Wahlenberg, 1818), Form C. All Slite Beds, Slite Marl. Follingbo 7 (14), Follingbo 8 (15), Slite 'a' (11), Snäckarve (6), Valbytte 1 (8–10, 12), Valbytte 3 (7), Valleviken 1 (13). 6, Ar52298, dorsal view of incomplete exoskeleton, glabellar tuberculation displaced leftward, ×1·5. 7*a*–*c*, Ar51786, anterior, oblique anterolateral, and dorsal views of incompletely enrolled specimen, *a*, ×3·5, *b*, *c*, ×3. 8, Ar52290, dorsal view of incomplete large cranidium, ×2. 9, Ar52291, dorsal view of pygidium, ×4. 10, Ar51787, exterior view of enrolled specimen, ×3. 11, Ar30643, dorsal view of pygidium, note large tubercles and unusually wide mucro, ×2·5 (coll. G. Lindström). 12, Ar52292, dorsal view of small pygidium, ×10. 13*a*, *b*, Ar52295, lateral and exterior views of labral plate, ×4. 14, Ar52297, exterior view of free cheek, ×3. 15, Ar51791, dorsal view of incomplete exoskeleton, ×4.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *punctatus*

non 1962 *Encrinurus punctatus* (Wahlenberg, 1821); Maksimova, p. 155, pl. 18, figs. 4 and 5 [With synonymy list].
. 1972 *Encrinurus* (*E.*) cf. *punctatus* 1; Schrank, p. 38, pl. 10, fig. 12.
. 1973 *Encrinurus tuberculatus* (Buckland 1836); Clarkson and Henry, p. 118, figs. 12, 16A–D.
. 1974 *Encrinurus punctatus;* Stemvers—van Bemmel, p.14, fig. 24.
? 1975 *Encrinurus punctatus* (Wahlenberg), 1821; Balashova, p. 111, pl. 1, fig. 23.
. 1978 *Encrinurus punctatus* (Wahlenberg); Männil, p. 109, pl. 1, figs. 1–7; pl. 2, figs. 1–6. [With synonymy list.]
v. 1981 *Encrinurus tuberculatus* (Buckland, 1836); Thomas, p. 64, pl. 18, figs. 1 and 3.
. 1982*b* *Encrinurus punctatus* (Wahlenberg, 1821); Männil, p. 53, pl. 4, figs. 1–3 [copy Männil 1978].

Remarks. This species has been mentioned countless times in literature, and the synonymy list includes only the most important references (further synonymy accepted here is found in the lists indicated above).

Lectotype. Specimen in the Palaeontological Institution, University of Uppsala, no. PIU G1200, a pygidium figured by Wahlenberg 1818, pl. 2, fig. 1*, designated as lectotype and figured by Tripp and Whittard 1956, pl. 3, figs. 1 and 2; from an unknown locality on Gotland, probably Högklint Beds.

Additional material. All material or localities of this common species cannot be listed here, but some locality data are included in 'Remarks on distribution'. Norwegian material previously referred to this species has not been studied here. The stratigraphical ranges of the three forms here included in *punctatus* are as follows:

Form A (the 'type' form). On Gotland this form first occurs together with *E.* (*E.*) *laevis* in beds belonging to the top of the Upper Visby Beds or base of the Högklint Beds. It is very common in the Högklint Beds, units a–d, and it ranges into the oldest part of the Slite Marl. Form A is also common in the British Wenlock.

Form B. This is the most common trilobite in the upper part of the Jaani Stage on Saaremaa, Estonia, and a large collection has been studied.

Form C. Known only from the Slite Beds on Gotland; from the northwestern part of the Slite Marl to the 'Pentamerus gothlandicus Beds'. *E.* (*E.*) *punctatus* Form C is the most common trilobite at all localities in this part of the Gotland sequence.

Diagnosis. Glabella not depressed below cheeks posteriorly. Anterior cranidial border with eight or ten tubercles, rarely one additional central. 1L small, not tuberculate abaxially, tubercle-pair I-1 very rare. Tubercles on field of free cheek prominent. Pygidium with twenty-five to thirty-two rachial rings. R/P ratio 2·5–3·0. Mucro about one sixth to one half length of rachis.

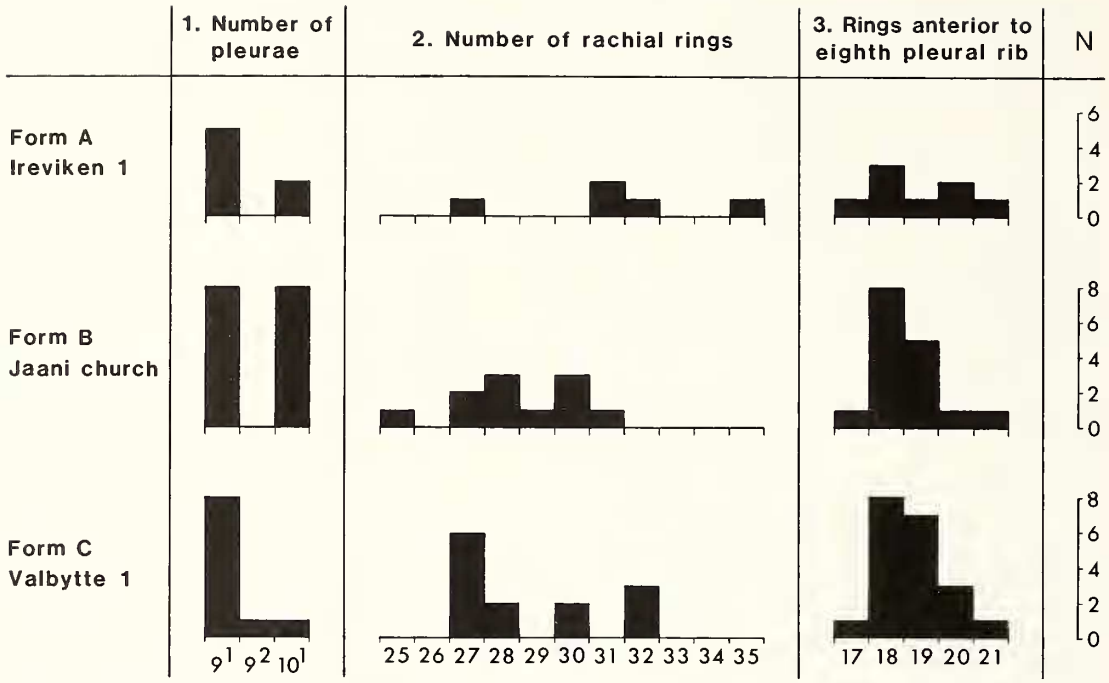
Description. The distinguishing features in the cephalon of the three different forms included here in *E.* (*E.*) *punctatus* are listed in Table 1. The thorax and pygidium are very similar in the different forms; a comparison of certain pygidial features is given in text-fig. 4.

Discussion. E. (*E.*) *punctatus*, as conceived here, is an extremely variable species. However, variation within each of the three morphological forms is small, and there is only slight or no overlap between the forms (Table 1). In spite of this it is uncertain if a splitting of *punctatus* into three formal subspecies or species would better reflect the original, biological relationships, and the practical advantages gained by a splitting are regarded here as too small to warrant such a step.

The British Wenlock *E.* (*E.*) *tuberculatus* is clearly synonymous with *punctatus* (though a neotype has not yet been designated for *tuberculatus*). Most major British collections have been studied, and the material belongs to *E.* (*E.*) *punctatus* Form A. This is so with most of the specimens figured as *E. tuberculatus* by Tripp (1962), but one specimen (pl. 66, fig. 7) has prominent, tuberculiform 1L and is not conspecific with the other material; this is also the case with one of the pygidia (Tripp 1962, pl. 68, fig. 5). All Estonian Jaani material figured by Rosenstein (1941) and Männil (1978) belongs to *E.* (*E.*) *punctatus* Form B, as does a large collection in Riksmuseum from the Jaani Stage of Saaremaa. Form B is coeval with one or both of Forms A and C, but a precise correlation is difficult. Morphologically, Form B is intermediate between Forms A and C. The pygidium from the Podolian Lower Wenlock figured by Balashova (1975) may well belong to Form A, but cannot be firmly assigned until a Podolian cranidium is figured.

TABLE 1. Comparison of the main distinguishing features of the three forms of *Encrinurus* (*Encrinurus*) *punctatus*.

Characters \ Horizons and localities	FORM A	FORM B	FORM C	
			Slite Marl	
	Wenlock Series, Dudley Högklint Beds units a–d Slite Marl, lowest part	Jaani Stage, Saaremaa	Valbytte 1–2	Follingbo 7–8
1. Number of large tubercles on anterior border of cranidium	eight, very rarely ten	eight, very rarely ten	ten	ten
2. Adaxial margin of eye (a.m.e.)	well abaxial to PL	barely to well abaxial to PL	slightly abaxial to PL	exsagittal to PL
3. Distance posterior margin of eye (p.m.e.) – posterior border furrow	larger than diameter of eye at base	less than or equal to diameter of eye at base	less than or equal to diameter of eye at base	less than diameter of eye at base
4. Eye stalk at base	strongly constricted	constricted	fairly to weakly constricted	weakly constricted
5. CT1 exsagittal position	posterior to p.m.e.	transverse or anterior to p.m.e.	just posterior to just anterior to p.m.e.	anterior to p.m.e.
6. CT2 transverse position	well abaxial to exsagittal of a.m.e.	well abaxial to exsagittal of a.m.e.	exsagittal of a.m.e.	exsagittal to adaxial of a.m.e.
7. Tubercles between CT2 – rachial furrow	one to three	none, very rarely one	none	none
8. Distance CT2 – CT4	about 1.2 – 1.5 times distance CT1 – CT2	about 1.4 – 1.6 times distance CT1 – CT2	about 2.0 times distance CT1 – CT2	about 2.0 times distance CT1 – CT2
9. Genal spines in dorsal view	curved	gently curved	straight to gently curved	straight
10. Border of free cheek	narrow	narrow	wide	wide
11. Shape of precranidial lobe	low, elongate	low, elongate	high	high
12. Tuberculation on anterior border of cranidium and on precranidial lobe	sparse, large, tall tubercles	sparse, large, tall tubercles	numerous small, low tubercles	numerous small, very low tubercles
13. Rostral plate	low, wide, rectangular to wedge-shaped, lower part tubercle-shaped, protruding	low, wide, rectangular to wedge-shaped, lower part tubercle-shaped, protruding	high, narrow, wedge-shaped, not tuberculate or protruding	high, shape unknown



TEXT-FIG. 4. Comparison of certain pygidial features of the three forms of *Encrinurus* (*Encrinurus*) *punctatus*. The number of rachial rings anterior to the eighth pleural pair (column 3) is the same as that used for calculating the R/P ratio.

Encrinurus (*Encrinurus*) *intersitus* sp. nov.

Plate 39, figs. 1–9; Plate 42, figs. ?12 and ?13; Plate 45, figs. ?12, 13, ?14, ?15

v. 1962 *Encrinurus macrourus* Schmidt; Tripp, pl. 67, fig. 1; pl. 68, fig. 2 [other figured specimens = *E.* (*E.*) *macrourus*]

v. 1978 *Encrinurus macrourus* Schmidt; Männil, pl. 2, fig. 9 [other figured specimens = *E.* (*E.*) *macrourus*].

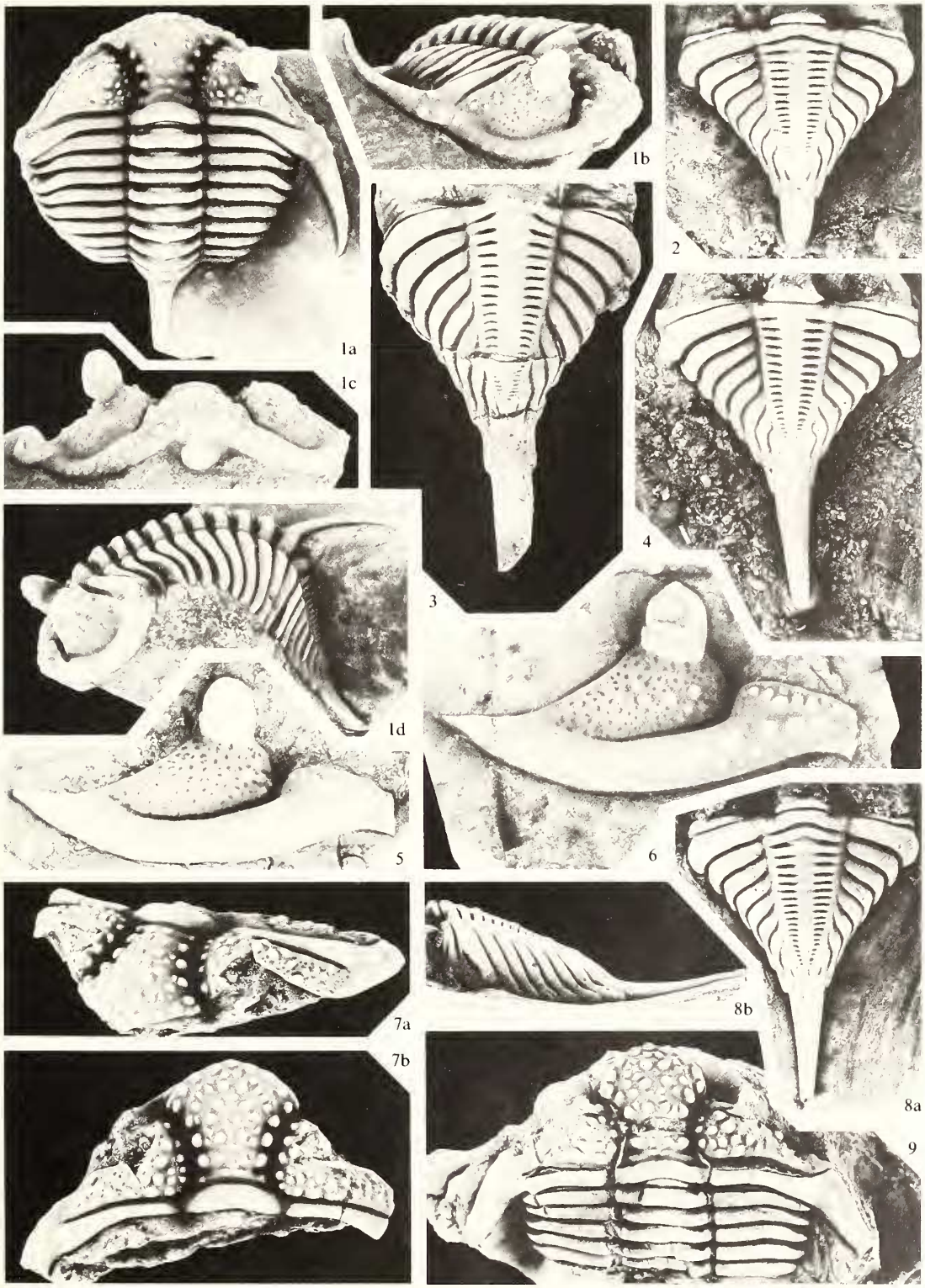
Name. Latin *intersitus*, in intermediate position; referring to the geographical and stratigraphical position between *E.* (*E.*) *macrourus* and *E.* (*E.*) *stubblefieldi*.

Holotype. Ar49041, broken cranidium with five thoracic segments (Pl. 39, fig. 9), from Likmide, 1, Hemse parish, Hemse Marl NW.

EXPLANATION OF PLATE 39

Figs. 1–9. *Encrinurus* (*Encrinurus*) *intersitus* sp. nov. Hemse Beds, Hemse Marl NW (1, 3, 4, 9), Hemse Marl SE (2, 5–8). Hulte 3 (2, 5–8), Likmide 1 (4, 9), Lukse 2 (3), field 100 m north-east of Vakten 1 (1). 1*a–d*, Ar52477*, dorsal, oblique anterolateral, anterior, and lateral views of complete exoskeleton, ×4. 2, Ar52476*, dorsal view of pygidium, note aberrant short, rounded mucro, ×3. 3, Ar52479*, exterior view of slightly worn pygidium, ×2·5. 4, Ar51779*, dorsal view of pygidium, ×3 (coll. C. Pleijel 1974). 5 and 6, exterior view of free cheek. 5, Ar52472*, ×2·3. 6, Ar52473*, ×3. 7*a*, *b*, Ar52474*, oblique anterolateral and dorsal views of incomplete cranidium, ×3. 8*a*, *b*, Ar52475*, dorsal and lateral views of pygidium, ×3. 9, Ar49041, dorsal view of holotype cranidium with part of thorax, ×2 (coll. C. Pleijel 1974).

* Paratypes.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *intersitus*

Paratypes. Apart from the figured specimens there are large collections in Riksmuseum and SGU, and all material cannot be listed, but specimens in Riksmuseum are labelled as paratypes.

Localities. This species is common at several localities in the Hemse Marl (text-fig. 9), although material from the northern and eastern localities is slightly different from the main type, and cannot be assigned confidently to this species. Positively identified specimens come from the following localities: Hemse Marl NW: Hablingbo parish—Lilla Hallvards 6, Lilla Hallvards 7, Lukse 1, Lukse 2, field at the road junction 100 m NNE of Vakten 1; Havdhem parish—Hemmungs 1, Kvinnegårda; Hemse parish—Likmide 1. Hemse Marl SE: Burs parish—Västlaus 1; Hemse parish—Hulte 3. Localities with questionably assigned specimens: Klinteberg Beds, Klinteberg Marl: Gerum parish—Ajmunde 1. Hemse Marl NW: Fardhem parish—Gardarve 1, Gerete 1, 250 m south of Gårdsby; Linde parish—Amlings 1; Lye parish—well by the road at the southern Medebys farm; Silte parish—Mästermyr 1. Hemse Marl SE and Hemse Beds, upper part: Burs parish—Hägvide 3; Linde parish—Rangsarve 1; Lojsta parish—Ase 1, Klints 1; När parish—Nyan 3, Öndarve 1; Rone parish—Sigdes kanal (probably = Sigdes 1).

Diagnosis. Glabella weakly convex, set well below cheeks posteriorly. Anterior cranidial border with nine tubercles, rarely eight. IL large, usually with tubercle abaxially. Tubercle-pair I-1 typically present. Eyes set wide apart. Genal spines and spine on tenth thoracic segment very long and stout. Tubercles on field of free cheek small. Pygidium with twenty-one to twenty-five rachial rings. R/P ratio 2·0–2·3. Mucro at least as long as rachis.

Discussion. This species is characterized by the following features in addition to those listed in the diagnosis: the wide cephalon, width:length ratio 2·8:1–3·0:1, the large and densely pitted field of free cheek, and the distinct tips of the seventh pleural pair proximally on the mucro.

This is an easily identified species in the southwestern localities, where *intersitus* replaces *macrourus* without overlap. The species can be followed towards the north-east through the localities Likmide 1, Hulte 3, and Västlaus 1. North of this occurs a slightly different form in beds that are probably slightly older. This form, best studied in material from Ajmunde 1 (Pl. 42, fig. 12), Amlings 1, and Gardarve 1 (Pl. 42, fig. 13) differs from the southwestern material mainly in the more elongated pygidium with shorter mucro. Although the pygidium, and to some extent the free cheek, is actually closer to *E.* (*E.*) *macrourus* ('Snoder type'; text-fig. 5c) than to *intersitus*, the cranidium is clearly of *intersitus* type. At present the form is best referred to as *E.* (*E.*) cf. *intersitus*. Specimens from localities further north-east, in probably slightly younger beds (Ase 1, Klints 1), again have long mucro, but are poorly preserved. The material from eastern localities (Hägvide 3, Nyan 3, Öndarve 1, Sigdes kanal) is incomplete but most similar to *intersitus* among Gotland *Encrinurus*, and is referred provisionally to that species.

E. (*E.*) *intersitus* sp. nov. differs from the youngest form of *E.* (*E.*) *macrourus* (text-fig. 5e) by the stout genal and thoracic axial spine, the shape and tuberculation of the free cheek, fewer

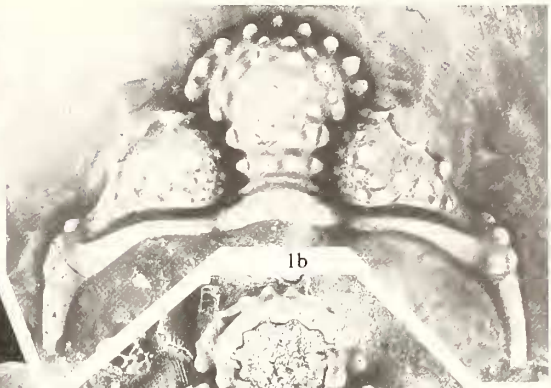
EXPLANATION OF PLATE 40

Figs. 1, 3–13. *Encrinurus* (*Encrinurus*) *jarkanderi* sp. nov. All Hemse Beds, unit b. Djaupviksudden 1 (3, 12), Gyle 1 (8). 'Kräklingbo' (11), Vidfälle 1 (1, 4, 6, 7, 9, 10), just south of 2 in point 22·5 near Kräklingbo (5), east of road 0·9 km north of Kräklingbo (13). 1*a*, *b*, Ar52327, oblique anterolateral and dorsal views of holotype cranidium, ×3·5. 3, LO 5700*, dorsal view of incomplete cranidium, ×3 (coll. J. E. Hede). 4, Ar52330*, dorsal view of pygidium, ×6. 5, SGU 5046*, exterior view of free cheek border, ×4 (coll. J. E. Hede 1919). 6, SGU 5047*, dorsal view of cranidium, ×3 (coll. H. Munthe 1908). 7. Ar52329*, anterior view of thoracic segment, ×5 (coll. L.-I. Jarkander 1984). 8, SGU 5048*, oblique lateral view of pygidium, ×6 (coll. J. E. Hede 1922). 9, Ar52328*, exterior view of free cheek, ×3·5. 10*a–c*, Ar52331*, dorsal, posterior, and lateral views of pygidium, ×4 (coll. L.-I. Jarkander 1984). 11, Ar30731*, dorsal view of pygidium, ×3. 12 and 13 exterior view of free cheek. 12, SGU 5049*, ×3·5 (coll. J. E. Hede 1923). 13. SGU 5050*, ×4.

Fig. 2. *Balizoma obtusus* (Angelin, 1851), Form B. Ar52341, dorsolateral view of complete, distorted specimen, Mästermyr 1, Hemse Beds, Hemse Marl NW, ×2.

* Paratypes.


1a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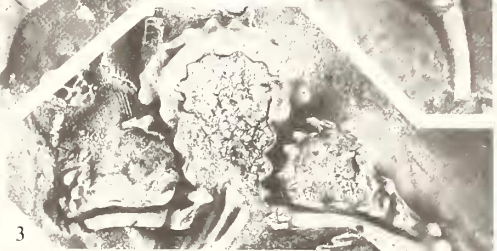
2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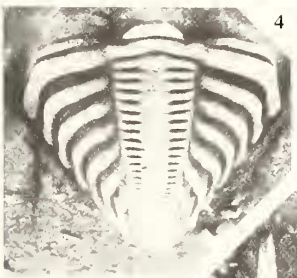
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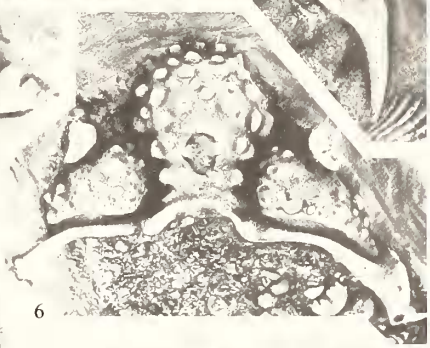
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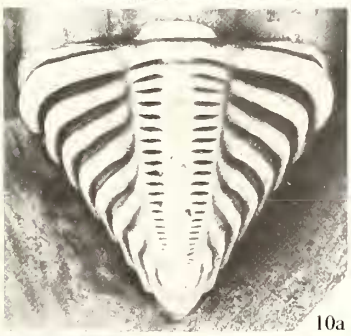
8

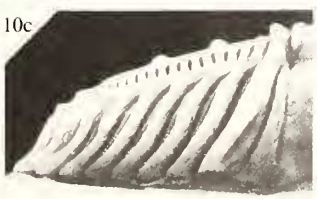

9


10a


11


12


10b


10c


13

RAMSKÖLD, *Encrinurus*, *Balizoma*

rachial rings in the pygidium, and a markedly larger size. *E.* (*E.*) *stubblefieldi* is similar to *intersitus* in several features, especially in the shape of the glabella, the short and wide cranidium, the stout genal and thoracic axial spine, and the long mucro. The labral plate of both species is apparently similar, but since the two species commonly occur together, isolated labral plates (Pl. 45, figs. 12, 14, 15) are difficult to assign to either species. *E.* (*E.*) *stubblefieldi* differs from *intersitus* in the subdued tuberculation, the shape of the free cheek, and the pygidium with fewer rachial rings and posterior pleural ridges that do not end in distinct tips on the pygidial margin.

Encrinurus (*Encrinurus*) *jarkanderi* sp. nov.

Plate 40, figs. 1, 3–13

Name. After Dr Lars-Ivar Jarkander who collected well-preserved material of this species.

Holotype. Ar52327, cranidium (Pl. 40, fig. 1), from Vidfälle 1, Kräklingbo parish, Hemse Beds, unit b.

Paratypes. All material is from Hemse Beds, unit b. Ala parish—Gyle 1 (SGU 5048). Kräklingbo parish—Djaupviksudden 1 (Ar52333–52334, LO 5700, SGU 5049), Hagrummet 1 (SGU 5057), Österby 1 (SGU 5052), Vidfälle 1 (Ar52328–52332, SGU 5047), east of road 0·9 km north of Kräklingbo church (SGU 5050), just south of *2* in point *22*.5 near Kräklingbo (SGU 5046), 'Kräklingbo' (Ar30731). One specimen (Ar30562) from Gutenviks, Östergarn parish, may be from Hemse Beds unit c. In total five cranidia, four free cheeks and seven pygidia.

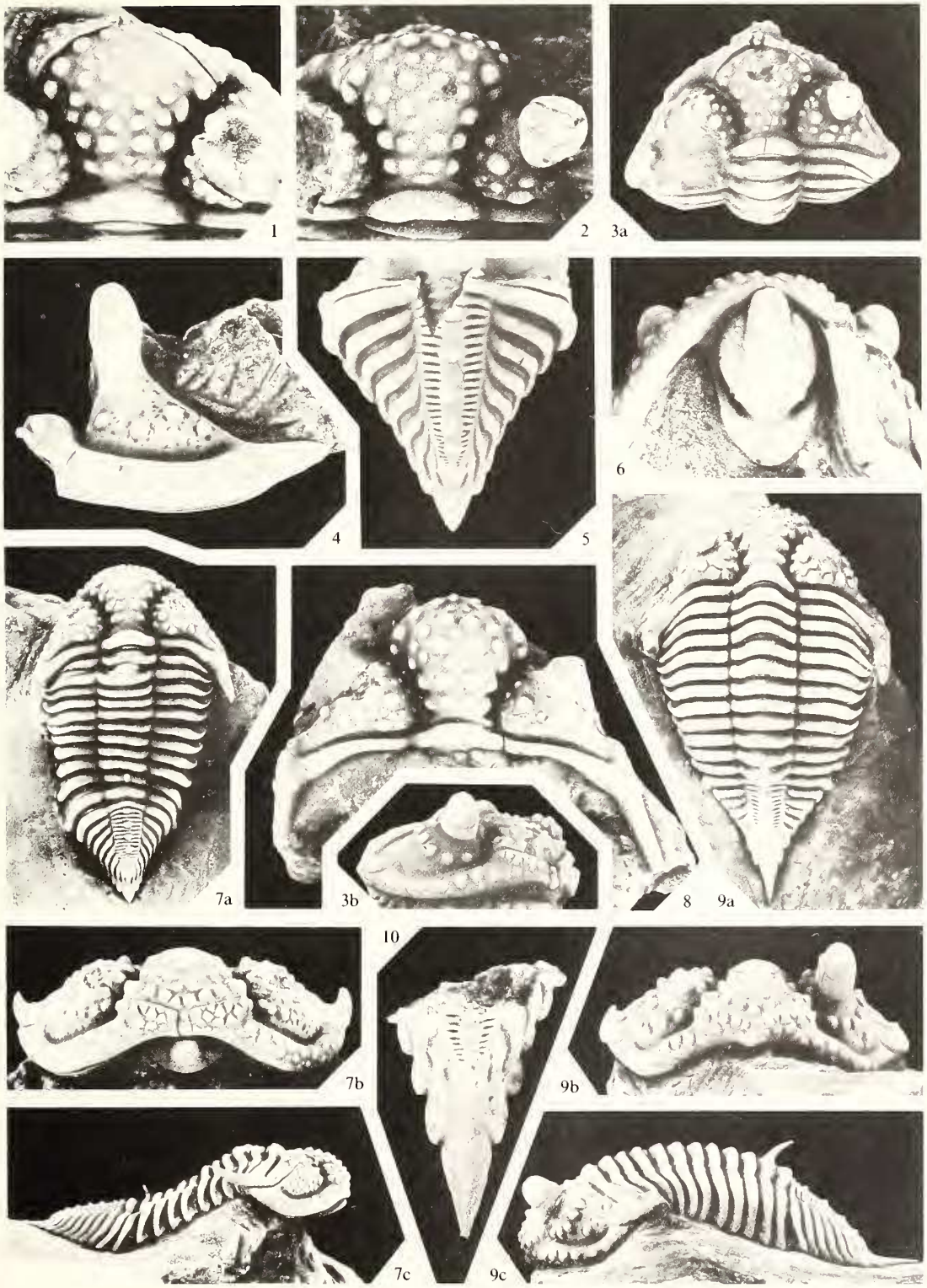
Diagnosis. Usually nine, sometimes ten tubercles on anterior cranidial margin. 1L small, no tubercle abaxially. Tubercle-pair 1-1 absent. Eyes set wide apart. Tubercles on field of free cheek prominent, precranidial lobe low, elongate, main tubercle row on border prominent. Pygidium with 24–29 rachial rings. R/P ratio 2·3–2·7. Mucro very small, 5–10 % length of rachis.

Description. Only characteristic features are described. 1L continuing as a narrow band across glabella (Pl. 40, figs. 1*b* and 6). Two tubercles anteriorly between eye and rachial furrow. At least three large tubercles at base of genal spine. Lateral border of free cheek with main tubercle row almost straight, tubercles very large, posterior row along suture with about five distinct tubercles. Precranidial lobe with about eleven tubercles roughly arranged in two to three oblique rows. Rostral plate not known, rostral suture short (dorsoventrally). Thorax known from isolated segments; at least one stout axial spine, presumably on tenth segment. Pygidium highly vaulted, usually 9^1 pleurae, occasionally 10^1. Tips of sixth and seventh pleural ribs weakly defined on margin. Interpleural furrows wide (exsag.), anterior pleural ridge distinct in anterior five furrows.

Discussion. This species is most easily recognized by the characteristic free cheek tuberculation combined with anterolaterally set eyes and a short-tipped pygidium. These features also distinguish *E.* (*E.*) *jarkanderi* from the otherwise rather similar *E.* (*E.*) *macrourus* and *E.* (*E.*) *nasutus* (see these species below). *E.* (*E.*) *jarkanderi* is unusual in its subgenus in having 1L and 2L that can be traced across the glabella, defined by faint, elongate depressions. These are, however, too weak to be regarded as truly continuous 1S and 2S.

EXPLANATION OF PLATE 41

Figs. 1–10. *Encrinurus* (*Encrinurus*) *macrourus* Schmidt, 1859. Mulde Beds, lower part (4, 5, 8), Hemse Beds, Hemse Marl NW (1–3, 6, 7, 9, 10). Blåhäll 1 (4, 5, 8), Eske 1 (9), Smissarve 1 (3), Snoder 1 (6, 10), Snoder 2 (1, 2), Urgude 3 (7). 1 and 2, dorsal view of glabella of complete specimen. 1, Ar52463, note tubercle iii-0, ×5. 2, Ar52464, ×6·5 3*a*, *b*, Ar52452, dorsal and anterolateral views of enrolled specimen, ×3. 4, Ar52456, exterior view of free cheek, ×4. 5, Ar52459, dorsal view of pygidium, ×4. 6, Ar52461, ventral view of labral plate of complete specimen, ×4. 7*a–c*, Ar51789, dorsal, anterior, and lateral views of complete specimen, note indistinct sagittal band, *a*, *c*, ×3, *b*, ×5. 8, Ar52455, dorsal view of cranidium, ×4. 9*a–c*, Ar51790, exterior, anterior, and lateral views of complete specimen, *a*, *c*, ×2·5, *b*, ×3. 10, Ar52462, dorsal view of large incomplete pygidium, ×4.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *macrourus*

E. (E.) jarkanderi is known with certainty only from Hemse Beds unit b, which must be synchronous with part of the Hemse Marl NW. However, trilobite faunas from these two units are very different and cannot be correlated precisely with each other.

Encrinurus (*Encrinurus*) *macrourus* Schmidt, 1859

Plate 41, figs. 1–10; Plate 42, figs. 1–11; text-fig. 5

* 1859 *Encrinurus punctatus* var. *macrourus* Schmidt, p. 438.
. 1941 *Encrinurus punctatus* (Wahlenberg) 1821; Rosenstein, text-fig. 4A, pl. 2, fig. 4–4*b*.
v. 1962 *Encrinurus macrourus* Schmidt; Tripp, p. 469, pl. 65, figs. 1, 3, 4; pl. 66, fig. 1*a–c;* pl. 67, figs. 2–4; pl. 68, figs. 1, 3, ?9; *non* pl. 65, fig. 2 [= *E. (E.) punctatus*]; pl. 67, fig. 1; pl. 68, fig. 2 [= *E. (E.)* cf. *intersitus* sp. nov.].
. 1972 *Encrinurus (E.)* cf. *punctatus* 2; Schrank, p. 38, pl. 11, fig. 4 [figs. 1, 2, 7 = paratypes of *E. (E.) ruhnueusis* Männil, 1978; figs. 3, 5, 6 indeterminable].
non 1972 *Encrinurus (E.) punctatus macrourus* Schmidt, 1859; Schrank, p. 42, pl. 12, fig. 6 [? = *E. (E.) ruhnuensis* Männil, 1978], fig. 7 [? = *E. (E.) punctatus*].
non 1972 *Encrinurus (E.)* cf. *punctatus macrourus* Schmidt, 1859; Schrank, p. 43, pl. 13, figs. 1, 2 [= *E. (E.) balticus* Männil, 1978].
1977 *E. macrourus* Schmidt, 1859; Schrank, p. 112.
v. 1978 *Encrinurus macrourus* Schmidt; Männil, pl. 2, figs. 7, 8, *non* fig. 9 [= *E. (E.) intersitus* sp. nov.].
1980 *Encrinurus macrourus* Schmidt, 1859; Strusz, p. 56, text-fig. 15 [but note that the cephalon is drawn from specimen of Schrank 1972, pl. 12, fig. 6, ? = *E. (E.) ruhnueusis* Männil, 1978].
1982 *Encrinurus macrourus* Schmidt; Alberti *et al.*, p. 32.
1982a *Encrinurus macrourus*; Männil, p. 65.

Lectotype. Specimen in the Geological Institute, Tallinn, Estonia, no. Tr 1905, incomplete thorax and pygidium from Petesvik, Hablingbo parish, Hemse Marl NW, selected and figured by Tripp 1962, pl. 67, fig. 4; refigured Männil 1978, pl. 2, fig. 7.

Remarks. Through the courtesy of Dr. Reet Männil in Tallinn I have been able to study Schmidt's Petesvik material (syntypes), and all specimens but one (see below) are conspecific. Schmidt (1859) also listed *E. punctatus* var. *macrourus* from several localities in the Hemse Beds apart from Petesvik. Pygidia with long mucro from these other localities do not belong to *macrourus* but to *E. (E.) stubblefieldi* or *E. (E.) intersitus* sp. nov. Schmidt's taxon was not used until Tripp (1962) revived it and selected a Petesvik specimen as lectotype. The original Petesvik locality is now inaccessible for recollecting. However, well-preserved material from nearby Lilla Hallvards 4, at the southern end

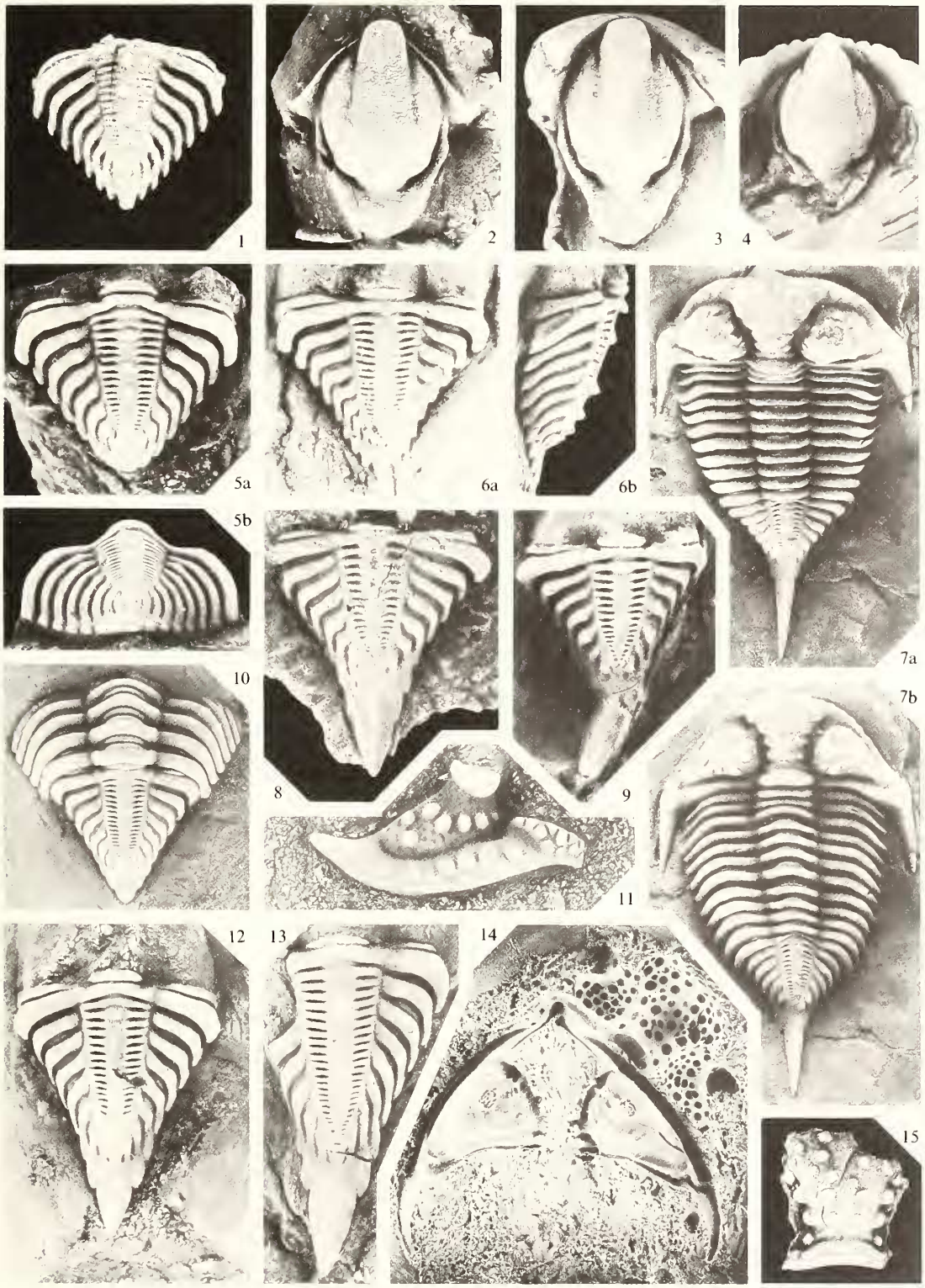
EXPLANATION OF PLATE 42

Figs. 1–11. *Encrinurus* (*Encrinurus*) *macrourus* Schmidt, 1859. Mulde Beds, lower part (1–3), undifferentiated (6), Hemse Beds, Hemse Marl NW (4, 5, 7–11). Blåhäll 1 (1–3), Djupviksvägen 1 (6), Hägsarve 4 (11), Lilla Hallvards 4 (7, 9), Petesvik (4), Smissarve 1 (8), Urgude 3 (5, 10). 1, Ar52460, exterior view of small pygidium, ×11. 2–4, exterior view of labral plate. 2, Ar52458, ×5. 3, Ar52457, ×4. 4, Ar30438, complete specimen, ×5 (coll. G. Lindström). 5*a*, *b*, Ar52451, exterior and posterior views of pygidium, note the very short 'mucro', ×4. 6*a*, *b*, Ar52454, dorsal and lateral views of aberrant pygidium, with one extra pair of pleural ribs, ×6. 7*a*, *b*, Ar52350, complete specimen with pygidium and cephalon in dorsal views, ×3. 8 and 9, dorsal view of pygidium. 8, Ar52453, ×4. 9, Ar52349, mucro broken, ×6. 10, Ar52450, dorsal view of pygidium and part of thorax of complete specimen, ×4. 11, Ar52449, exterior view of free cheek, visual surface lost, ×4.

Figs. 12 and 13. *E. (E.)* cf. *intersitus* sp. nov. Dorsal view of pygidium. 12, Ar52465, Ajmunde 1, Klinteberg Beds, Klinteberg Marl, ×4. 13, Ar52466, incomplete, Gardarve 1, Hemse Beds, Hemse Marl NW, ×4.

Figs. 14 and 15. *E. (E.) uasutus* sp. nov. Eke Beds, upper part; Lau Backar 1. 14, Ar51792*, latex cast of cephalon and an additional cranidium, ×2·5. 15, Ar51793*, dorsal view of cranidial fragment, note the very sparse tuberculation, ×3.

* Paratypes.



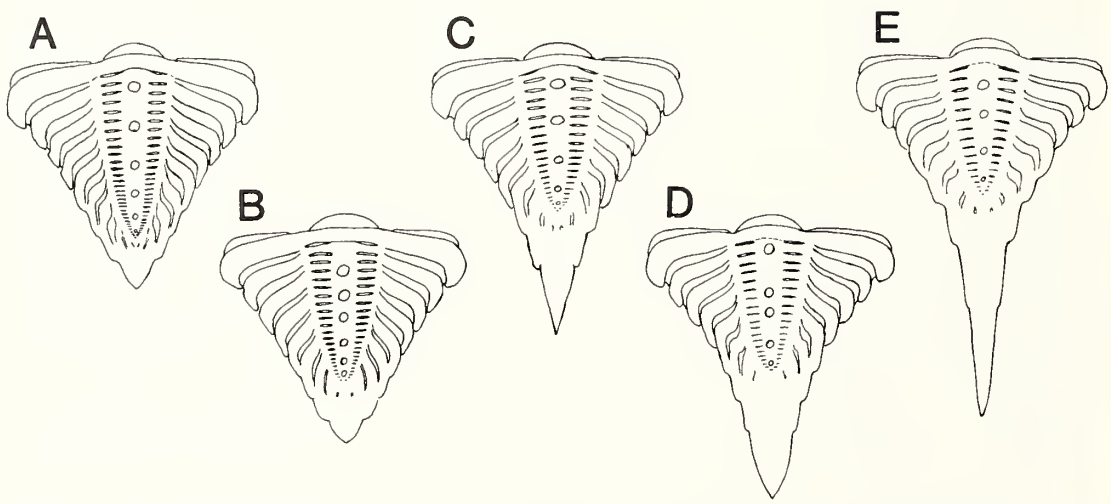
RAMSKÖLD, *Encrinurus* (*Encrinurus*)

of Petesvik, is morphologically identical to Schmidt's specimens. Two more of Schmidt's specimens have been figured; a cranidium (Männil 1978, pl. 2, fig. 8) and a pygidium, possibly not from Petesvik (Männil 1978, pl. 2, fig. 9); the latter apparently belongs to *E.* (*E.*) *intersitus* sp. nov.

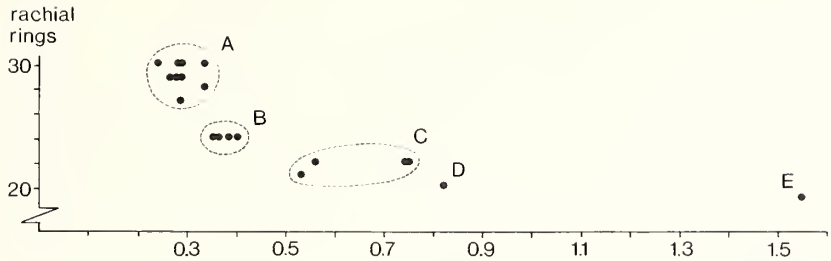
Additional material. Localities: Mulde Beds, lower part: Eksta parish—Blåhäll 1; Klinte parish—Värsände 1. Undifferentiated: Eksta parish— Djupviksvägen 1, Nordervik (635350 163845); Fröjel parish—Mulde Tegelbruk 1. Upper part: Fröjel parish—Haugklintar 1; Klinte parish—Loggarve 2. Klinteberg Beds, lower part: Loggarve 2. Hemse Beds, Hemse Marl NW: Hablingbo parish—Lilla Hallvards 4, 5, Petesvik; Levide parish—Levide 1; Silte parish—Mästermyr 1, Mickels 1, Smissarve 1, Snoder 2; Sproge parish—Eske 1, Hägsarve 2, 4, Snoder 1, Urgude 3, 4. Localities with too few or poor specimens to permit definite assignment: Mulde Beds, upper part: Fröjel parish—Däpps 1, 2. Klinteberg Beds, lower–middle part: Klinte parish—Klinteberget.

Diagnosis. Anterior cranidial border usually with nine, sometimes eight or ten tubercles. 1L small, no tubercle abaxially, tubercles 1-1 and iii-0 rare. Precranidial lobe low, field of free cheek with prominent tubercles. Slender axial spine or tubercle on tenth thoracic segment. Pygidium with seventeen to twenty-nine rachial rings. R/P ratio 2·3–2·9.

Description. Only features that may be of diagnostic value are described. Glabella weakly inflated, set below cheeks posteriorly. Anterior border of cranidium usually with nine tubercles (60–70 %), sometimes eight (*c.* 25 %), rarely ten (< 10 %). Tubercle iii-0 present in less than 10 % of specimens. Tubercle I-0 fairly common (*c.* 35 %). Tubercle row VI invariably present. 1L ridge-shaped, sometimes almost reaching sagittal line. Eye pedunculate, height of stalk varying from equal to height of visual surface (Hemse Beds, Pl. 41, figs. 3 and 9) to 1·5 times that height (Mulde Beds, Pl. 41, fig. 4), eye-stalk only slightly constricted at base. Eye set close to rachial furrow, anteriorly one tubercle between eye and rachial furrow, distance to posterior border furrow less than or equal to diameter of eye (visual surface). Rostral plate (Pl. 41, figs. 3, 7, 9) two to three times as high as wide, with a tubercle centrally on upper half, lower half slightly protruding. Axial tubercle on seventh thoracic segment. Hemse Beds specimens sometimes with only a tubercle on tenth segment (Pl. 42, fig. 7), usually with a short, slender spine (Pl. 41, figs. 7 and 9); Mulde Beds specimens appear to have a slightly stouter spine. Pygidium (text-fig. 5) usually with 9^1 pleurae. Posterolateral tip of sixth pleura reaches as far back as end of rachis or longer, tips of all seven pleurae distinctly defined on margin. Mucro varying from (uniquely) a rounded knob (Pl. 42, fig. 5) to flat subtriangular (all Mulde Beds, most Hemse Beds specimens)



TEXT-FIG. 5. Chronologically arranged pygidia of *Encrinurus* (*Encrinurus*) *macrourus*. The lettering is the same as in text-figs. 6 and 9. All reconstructions are based on specimens of about equal size. A, Mulde Beds, Blåhäll 1. B, Hemse Marl NW, Urgude 3. C, Hemse Marl NW, Snoder 1 and 2. D, Hemse Marl NW, Smissarve 1. E, Hemse marl NW, Lilla Hallvards 4.



TEXT-FIG. 6. Diagram showing progressive change in the pygidium of *Encrinurus* (*Encrinurus*) *macrourus* towards fewer rachial rings and longer mucro. The scale on the abscissa is the ratio between the sagittal length of the rachis (excluding articulating half-ring) and the postrachial part of the pygidium (most of which is the mucro). The letters A–E indicate the localities of text-figs. 5 and 9. Pygidia of less than 7 mm total length have not been included.

to lancet-like, subtriangular in section (large Hemse Beds specimens, Pl. 41, figs. 9 and 10) to as long as rachis (Pl. 42, figs. 7 and 9). One small pygidium (Pl. 42, fig. 6) has eight pairs of pleurae reaching margin, similar to the specimen figured by Schrank (1972, pl. 11, fig. 6); this is considered abnormal.

Trends in variation. During the long range of this species some changes in morphology can be followed. The oldest (Mulde Beds) specimens have highly stalked eyes, deep rachial furrows, a fairly stout axial spine, about twenty-seven to thirty rachial rings in the pygidium, 9^1–10^1 pleurae, and a triangular mucro (text-fig. 5A). In the lower Hemse Marl NW, specimens still have deep rachial furrows, but lower eyes, a very slender axial spine, about twenty-two to twenty-five rachial rings, 9^1 pleurae, and a mucro ranging from triangular (lowermost Hemse Marl NW; text-fig. 5B) to lancet-shaped (slightly younger; text-fig. 5C). The type material (and Lilla Hallvards 4; text-fig. 5E) is the youngest of the species. It is characterized by shallow rachial furrows, an axial tubercle instead of spine, only seventeen to nineteen rachial rings, and 8^1 pleurae that are markedly extended posteriorly, so that the posterolateral tip of the fifth pleura reaches as far back as the end of rachis. From this a long mucro is produced; the seventh pleural pair reaches half its length, and the total length exceeds that of the pygidial rachis. The eye height is similar to low Hemse Marl NW material. There is thus a general trend in *macrourus* towards lower eyes, shallower rachial furrows, reduction of the thoracic axial spine, fewer rachial rings and pleurae in the pygidium, and a longer mucro.

Discussion. E. (*E.*) *macrourus* is one of the smallest Gotland *Encrinurus*, with a total length for extended specimens usually 25–30 mm. Very few specimens reach 40 mm, but a fragmentary pygidium (Pl. 41, fig. 10) indicates a total length of 49–50 mm. The small size was one criterion used by Tripp (1962) to distinguish *macrourus* from *punctatus*. Other differences from *punctatus* include the less inflated glabella, the smaller precranidial lobe, the rarity of tubercle iii-0 ($< 10\,\%$ compared to $> 90\,\%$), and the common occurrence of a median tubercle on the anterior cranidial border.

Pygidia of the Gotland form *E.* (*E.*) cf. *intersitus* sp. nov. (Pl. 42, figs. 12 and 13) show considerable similarities to some Hemse Beds specimens of *macrourus*. These pygidia are, however, associated with a type of cranidium much more similar to *intersitus* than to *macrourus*, being very wide and short and with densely tuberculate fixed cheeks. Better material is needed to clarify the relationship between this form, *intersitus* and *macrourus*. The middle Wenlock *E.* (*E.*) *ruhnuensis* Männil, 1978 from Estonian cores also closely resembles *macrourus*. It differs by its short, weak genal spines and tubercle iii-0 combined with eight tubercles on the anterior cranidial border, a pattern that has not been observed in *macrourus*.

Encrinurus (*Encrinurus*) *nasutus* sp. nov.

Plate 42, figs. 14 and 15; Plate 43, figs. 1–11

. 1967 *Encrinurus punctatus* Wahlenberg 1821; Hucke, pl. 28, fig. 8, *non* fig. 7 [= *Balizoma obtusus* (Angelin, 1851)].

. 1972 *Encrinurus* (*E.*) cf. *punctatus* 3; Schrank, p. 39, pl. 11, figs. 9 and 10, *non* fig. 8 [= *Balizoma obtusus* (Angelin, 1851)]; pl. 12, figs. 1–3; text-fig. 3.

Name. Latin *nasutus*, 'with nose'; referring to the nose-like profile of the rostral plate *in situ*.

Holotype. Ar30558, incomplete extended exoskeleton, Plate 43, fig. 1*a–c*, from Gannor 1, Lau parish, Eke Beds, lower part (local unit *d* of Hede *in* Munthe *et al.* 1925).

Paratypes. From the type locality: Ar30557, Ar30528–30529. From the upper Eke Beds at Lau Backar 1, Lau parish: Ar51781, Ar51792–51795, Ar52480–52485, and a large number of unnumbered, fragmentary specimens. Incomplete material (Ar52440–52447, Ar52467) from the Hemse Beds unit e, at Millklint/Torsburgen (Gammelgarn/Kräklingbo parishes) almost certainly also belongs to this species. Material from German Ludlow erratics described by Schrank (1972) as *E.* (*E.*) *punctatus* 3 is conspecific with *E.* (*E.*) *nasutus* sp. nov.

Diagnosis. Anterior cranidial border with nine or occasionally eight or ten tubercles. 1L large, with tubercle abaxially. Tubercle-pair I-1 commonly present. Occipital ring and thoracic segments with numerous distinct tubercles. Field of free cheek with small tubercles, precranidial lobe low, very elongate. Rostral plate with strongly protruding lower part. Pygidium with twenty-six to twenty-nine rachial rings. R/P ratio 2·3–2·6. Mucro lancet-shaped, about half length of rachis.

Description. Only characteristic features are described. 1L commonly traceable across glabella, tubercle I-0 or I-1 present in over 50 %. Tubercle ii-0 or ii-1 present in 100 %. Anterior cranidial border usually with nine tubercles (five specimens), occasionally eight or ten (one specimen each). Fixed cheek densely tuberculate adaxially and posterior to eye. One or two small 'tubercles' between PL and cranidial margin. Occipital ring with one central and two flanking tubercles. Precranidial lobe with about eleven tubercles. Labral plate with rhynchos bluntly subtriangular anteriorly. Weak axial tubercles on most thoracic segments, best developed on third, fifth, and seventh; tenth segment with a stout axial spine. A strong lateral tubercle on several segments. Pygidium with 9^1 pleurae. No variation observed in shape of mucro.

Discussion. This species is readily distinguished from all other Gotland *Encrinurus* by the combination of tuberculiform 1L and lancet-shaped mucro. A British cranidium figured by Tripp (1962, pl. 66, fig. 7) as *E. tuberculatus* (= *E.* (*E.*) *punctatus* here) appears indistinguishable from *nasutus*, but more complete material is needed for a firm assignment. *E.* (*E.*) *nasutus* is also known from German upper Ludlow erratics (*E.* (*E.*) cf. *punctatus* 3 of Schrank 1972).

EXPLANATION OF PLATE 43

Figs. 1–11. *Encrinurus* (*Encrinurus*) *nasutus* sp. nov. Eke Beds, lower part (1, 2, 7), upper part (3–6, 8–11). Gannor 1 (1, 7), Lau Backar 1 (3–6, 8–11), 'Lau Kanal' (2). 1*a–c*, Ar30558, dorsal, lateral, and anterior views of almost complete holotype, *a*, *b*, ×2·5, *c*, ×4. 2*a*, *b*, Ar30528*, dorsal and oblique anterolateral views of enrolled specimen, ×3. 3, Ar52482*, exterior view of labral plate, ×4. 4*a*, *b*, Ar51781*, anterior and dorsal views of incomplete cephalon, *a*, ×5, *b*, ×3. 5*a*, *b*, Ar52480*, anterior and dorsal views of enrolled specimen, *a*, ×6, *b*, ×4, only eight tubercles on anterior cranidial border. 6, Ar52485*, dorsal view of pygidium, ×6. 7, Ar30557*, dorsal view of cranidium and thorax, ×2·5. 8 and 9, dorsal view of pygidium. 8. Ar52483*, ×5. 9, Ar52484*, ×4. 10, Ar51795*, ventral view of pygidium, ×4. 11, Ar52481*, exterior view of free cheek, ×5.

* Paratypes.

RAMSKÖLD, *Encrinurus* (*Encrinurus*) *nasutus*

Encrinurus (*Encrinurus*) *odvaldensis* sp. nov.

Plate 44, figs. 1–13

Name. From the type locality.

Holotype. Ar52313, cranidium (Pl. 44, fig. 10), from Odvalds 1, Klinte parish, Slite Beds, 'Pentamerus gothlandicus Beds'.

Paratypes. From the 'Pentamerus gothlandicus Beds', Klinte parish–Odvalds 1 (Ar52314–52323), Robbjäns 1 (Br131177), Robbjäns 2 (Ar52300–52312), Svarvare 1 (Ar52324–52326), drainage ditch in C. Smitterberg's field (Ar30546). From field south-west of Gannarve, Fröjel parish (Ar30547), uncertain horizon. Three pygidia (Ar30671, Ar30687–30688) from ?Mulde Beds at Djupvik, Eksta parish, also belong to this species. In total four cranidia, five free cheeks, four labral plates, and twenty pygidia.

Diagnosis. Glabella sparsely tuberculate; tubercles iv-0, v-0, VI-0 typical. Anterior cranidial border with eight tubercles. 1L small, not tuberculate, tubercle-pair I-1 absent. Eye fairly highly stalked. Prominent tubercles on field of free cheek. Pygidium with twenty to twenty-two rachial rings. R/P ratio 2·4–2·6. Mucro equal in length to rachis. Seventh pleural pair extends well on to the mucro. All tuberculation coarse.

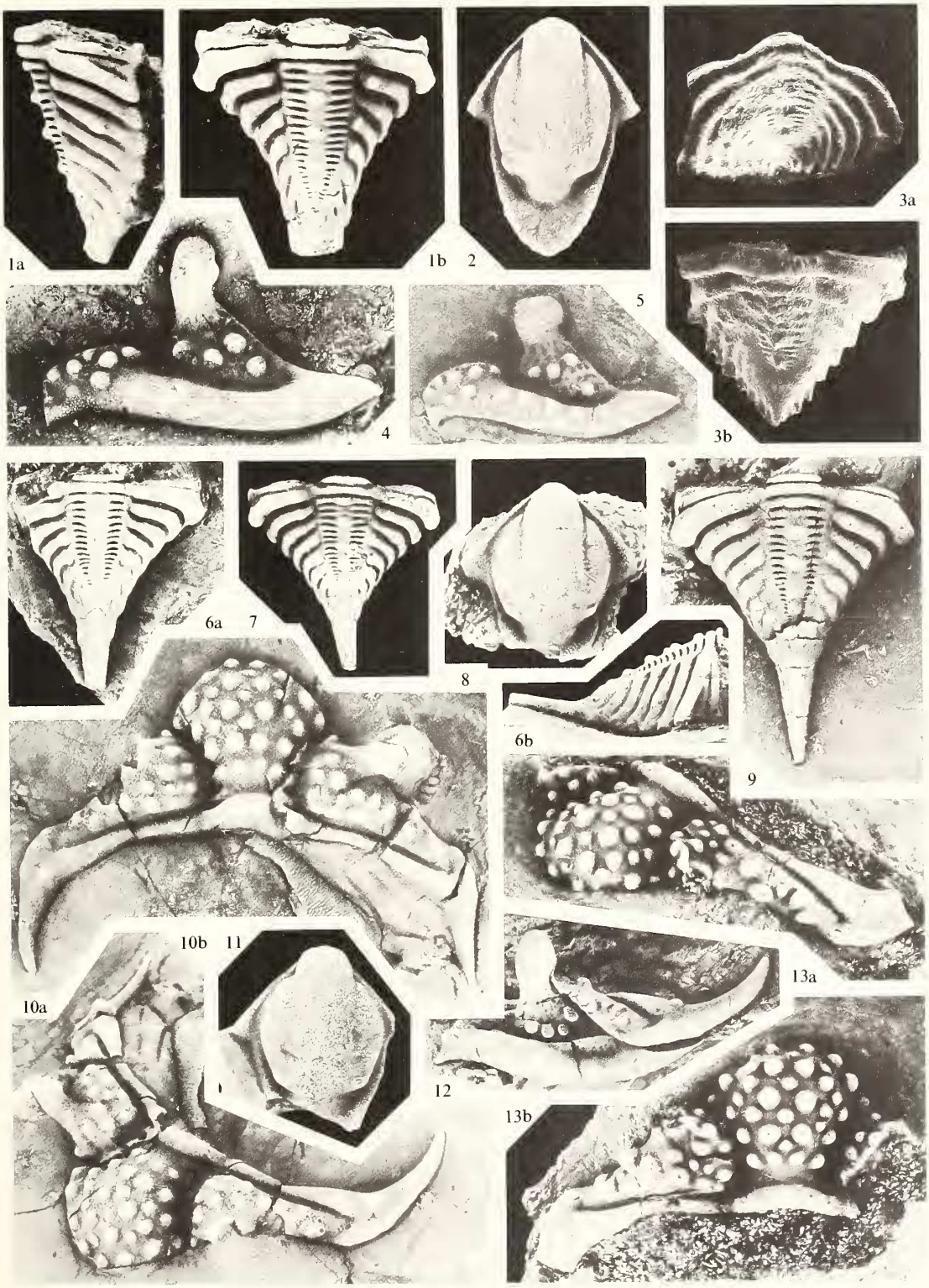
Discussion. This species is characterized by the reduced glabellar tuberculation, highly stalked eyes, and wide pygidium with long mucro. The pygidia are uniform in shape, number of rings and ribs, and length of mucro. Of the Gotland species it is most similar to *E.* (*E.*) sp. A, which is poorly known, but differs at least in the more elongate pygidium with more rachial rings. *E.* (*E.*) sp. A is probably only slightly older than *odvaldensis*. The Estonian Wenlock *E.* (*E.*) *balticus* Männil, 1978 closely resembles *odvaldensis*, but differs in the more elongate glabella (of *macrourus/intersitus* shape) with well-developed 1L carrying tubercle pair I-1, the less coarse tuberculation, larger number of tubercles on field of free cheek, and the pygidium with narrower rachis, seventh pleural pair set even farther posteriorly, and more slender, longer mucro (see also Schrank 1972, pl. 13, figs. 1 and 2; specimens included by Männil in *balticus*). *E.* (*E.*) *odvaldensis* is also remarkably similar to the American Wenlock *E.* (*E.*) *egani* Miller, 1880 (revised by Holloway 1980), especially in the reduced glabellar tuberculation, but in most other features as well. However, *egani* was interpreted as dimorphic by Holloway (1980), has much higher eye stalks, and the base of the mucro is raised above the plane of the pleural tips. *E.* (*E.*) *egani* is even closer to *E.* (*E.*) sp. A, with which it is compared in the discussion of that species.

E. (*E.*) *odvaldensis* is known with certainty only from the 'Pentamerus gothlandicus Beds', immediately below the Slite Siltstone, but may continue into beds following directly on the Slite Siltstone near the western coast of Gotland. This poorly known interval of the Gotland sequence includes the boundary of the Slite/Mulde Beds. The specimen from south-west of Gannarve and those from Djupvik probably originate from these strata. The distribution is otherwise restricted to

EXPLANATION OF PLATE 44

Figs. 1–13. *Encrinurus* (*Encrinurus*) *odvaldensis* sp. nov. Slite Beds, 'Pentamerus gothlandicus Beds' (1–6, 8–13), ?Mulde Beds, lowest part (7). Odvalds 1 (4, 5, 9, 10), Robbjäns 2 (1, 2, 8, 11, 13), Svarvare 1 (3, 6, 12), field south-west of Gannarve (7). 1*a*, *b*, Ar52304*, lateral and dorsal views of pygidium, ×4. 2, Ar52303*, exterior view of labral plate, ×5·5. 3*a*, *b*, Ar52326*, posterior and dorsal SEM views of last meraspid stage pygidium, ×35. 4 and 5, exterior view of free cheek. 4, Ar52314*, ×3. 5, Ar52315*, ×8. 6*a*, *b*, Ar52325*, dorsal and lateral views of pygidium, ×3 (coll. Amelang 1982). 7, Ar30547*, dorsal view of pygidium, ×5. 8, Ar52301*, exterior view of labral plate, ×5. 9, Ar52316*, dorsal view of pygidium, ×3. 10*a*, *b*, Ar52313, dorsal and oblique anterolateral views of holotype cranidium, ×3. 11, Ar52302*, exterior view of labral plate, ×4. 12, Ar52324*, anterolateral view of incomplete cephalon, ×3. 13*a*, *b*, Ar52300*, oblique anterolateral and dorsal views of incomplete cranidium, ×3.

* Paratypes.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *odvaldensis*

the southwestern part of the 'Pentamerus gothlandicus Beds', where this species is fairly common, and the only encrinurid; in the north-east these beds yield *E.* (*E.*) *punctatus* Form C.

Encrinurus (*Encrinurus*) *schisticola* Törnquist, 1884

Plate 45, figs. 1–9

v* 1884 *Encrinurus schisticola* Törnquist, p. 23, pl. 1, figs. 15–17.
. 1968 *Encrinurus schmidti* Männil, p. 273, pl. 1, figs. 1–5; pl. 2, figs. 1–5.

Lectotype. Selected here; LO 573 T, incomplete cranidium and thorax, figured Törnquist 1884, pl. 1, fig. 15, refigured here Plate 45, fig. 4, from the Retiolites shale (Kullatorp Stage, upper Llandovery), Styggforsen, Dalarna.

Remarks. Törnquist (1884, pl. 1, fig. 16) also figured a pygidium (LO 574 t) from the counterpart slab of the lectotype, possibly belonging to the same individual. The third specimen he figured is a pygidium (SGU 4187), also from the type locality.

Other material. In Sweden this species is known from the Retiolites shale at Styggforsen (Ar24675–24676) and Nittsjö in Dalarna (Ar24637–24638, Ar24643–24671, LO 5701–5705, and unnumbered material). In total eight cranidia, one labral plate, four free cheeks, eighteen pygidia, and numerous thoracic segments. A well-preserved pygidium (SGU 5056) from 100·2–101·3 m in the core from the boring at Visby Cement factory is indistinguishable from *E.* (*E.*) *schisticola*. The age is probably upper Llandovery (Dalip Sethi, pers. comm.). In Estonia this species is known from the Adavere Stage (Upper Llandovery), Konovere River, Lätiküla.

Diagnosis. See Männil 1968, p. 278 (diagnosis of *E. schmidti*).

Description. Only some minor details can be added to the comprehensive description of *E. schmidti* given by Männil (1968). As noted by Männil, there is a weak but distinct axial tubercle on each of the fifth, seventh, and tenth thoracic segments. This arrangement is likely to be homologous with the axial spines and tubercles present in later *E.* (*Encrinurus*) on the same segments. The number of rachial rings can be counted only in four Swedish pygidia (apart from the Visby core specimen which has 20 rings); these have 18, 18, 17, and 17 rings, compared with 19 or occasionally 20 in Estonian material. R/P ratio 2·0–2·3. 9^1 pleurae; last pair of furrows visible only in well-preserved specimens. Anterior pleural bands distinct.

Discussion. The Estonian specimens of *E. schmidti* Männil, 1968 agree completely morphologically with the Swedish material on which Törnquist (1884) erected *E. schisticola*. *E. schmidti* is accordingly regarded here as a junior subjective synonym of *E.* (*E.*) *schisticola*. This species is easily identified, and cannot be mistaken for any other described species. Männil (1968) recognized a morphological group of *E.* (*E.*) *schmidti*, including also *E. kiltsiensis* and *E. rumbaensis*, both described by Rosenstein (1941). Such a group is not recognized here, and the two latter species are referred to a different subgenus, *E.* (*Nucleurus*), from *E.* (*E.*) *schmidti*.

EXPLANATION OF PLATE 45

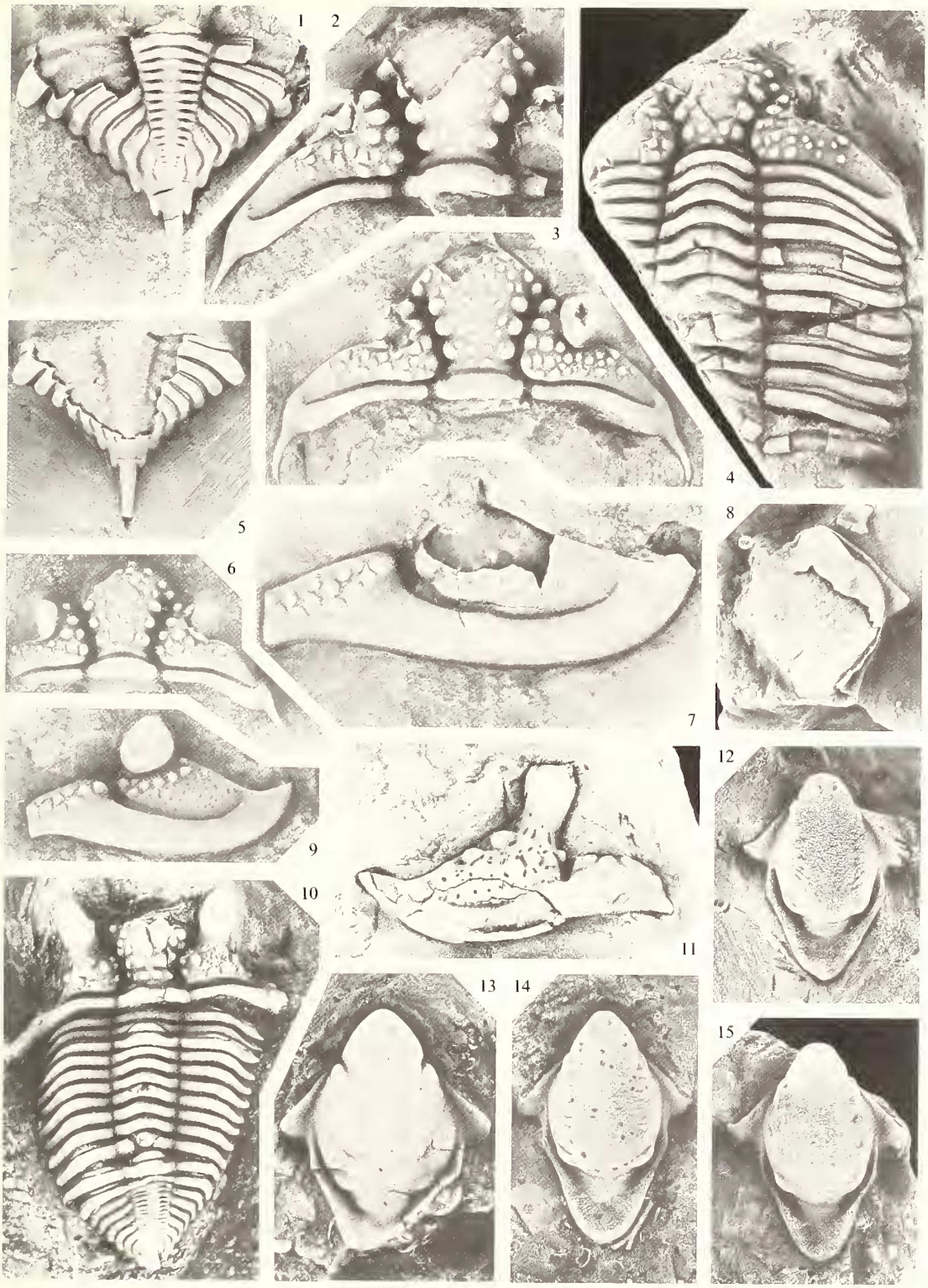
Figs. 1–9. *Encrinurus* (*Encrinurus*) *schisticola* Törnquist, 1884. All from Retiolites shale, Dalarna. Nittsjö (1–3, 5–9), Styggforsen (4). Figs. 1–5, 7 coll. S. L. Törnquist. 1, LO 5701, dorsal view of pygidium, ×3. 2 and 3, dorsal view of cranidium. 2, LO 5702, incomplete ×3. 3, LO 5703, ×4. 4, LO 573T, exterior view of lectotype incomplete cranidium and thorax, ×3. 5, LO 5704, dorsal view of pygidium, ×3. 6, Ar24664, dorsal view of small cranidium, ×6. 7, LO 5705, exterior view of free cheek, ×4. 8, Ar24658, exterior view of incomplete labral plate, ×4. 9, Ar24668, exterior view of small free cheek, ×6.

Figs. 10 and 11. *E.* (*E.*) sp. C? Both from Hemse Marl NW, Urgude 4. 10, Ar52281, dorsal view of almost complete exoskeleton, ×4. 11, Ar52280, exterior view of free cheek lacking visual surface, ×2.5.

Figs. 12, 14, 15. *E.* (*E.*) *intersitus* sp. nov. or *E.* (*E.*) *stubblefieldi* Tripp, 1962. All from the Hemse Marl SE or top. Gannor 3 (15), Västlaus 1 (14), unknown locality no. 1 (12). Exterior view of labral plate. 12, Ar52299, ×4. 14, Ar51769, ×4 (coll. G. Holm). 15, Ar51777, ×4.

Fig. 13. *E.* (*E.*) *intersitus* sp. nov. Ar51780*, exterior view of labral plate from Likmide 1, Hemse Marl NW, ×4 (coll. C. Pleijel 1974).

* Paratype.



RAMSKÖLD, *Encrinurus* (*Encrinurus*)

Encrinurus (*Encrinurus*) *stubblefieldi* Tripp, 1962

Plate 45, figs. ?12, ?14, ?15; Plate 46, figs. 1–14

v* 1962 *Encrinurus stubblefieldi* Tripp, p. 471, pl. 65, fig. 12, pl. 67, figs. 14 and 15; pl. 68, fig. 11.
non 1968*a* *Encrinurus stubblefieldi* Tripp; Balashova, p. 116, pl. 3 fig. 12.
. 1972 *Encrinurus* (*E.*) *stubblefieldi* Tripp, 1962; Schrank, p. 42, pl. 12, figs. 4 and 5 [with synonymy list].

Holotype. Specimen in the British Geological Survey, Nottingham, no. GSM 36846, internal mould of cranidium, from the 'Upper Ludlow shales', Whitcliff, Shropshire, England, figured Tripp 1962, pl. 65, fig. 12; pl. 67, fig. 15.

Material and localities. Outside England this species has been described from German Ludlow erratics (Schrank 1972). It is also present in the Podolian Ludlow (see below). On Gotland *stubblefieldi* is restricted to the Hemse Marl SE, belonging to the younger part of the Hemse Beds (lower/middle Ludlow). Material: One fairly complete exoskeleton and numerous (minimum twenty each) cranidia, free cheeks, labral plates, and pygidia. Localities: all Hemse Beds, Hemse Marl SE (and top?): Alva parish—Alva kanal, *c.* 100 m south-east of Överöstris farm; Burs parish—Hägvide 3, Djupträsk, Västlaus 1, Kärna kanal, drainage ditch south of Kålmans; Hablingbo parish—Leisungs 1; Hemse parish—Hulte 3; Lau parish—Botvide 1, Gannor 3, Gogs 1, Hallsarve 1, Tuten 1, ditch 500 m north-east of Lau church; När parish—Nyan 4; Näs parish—Klasård 1, vaktård 2; Rone parish—Sigdes kanal.

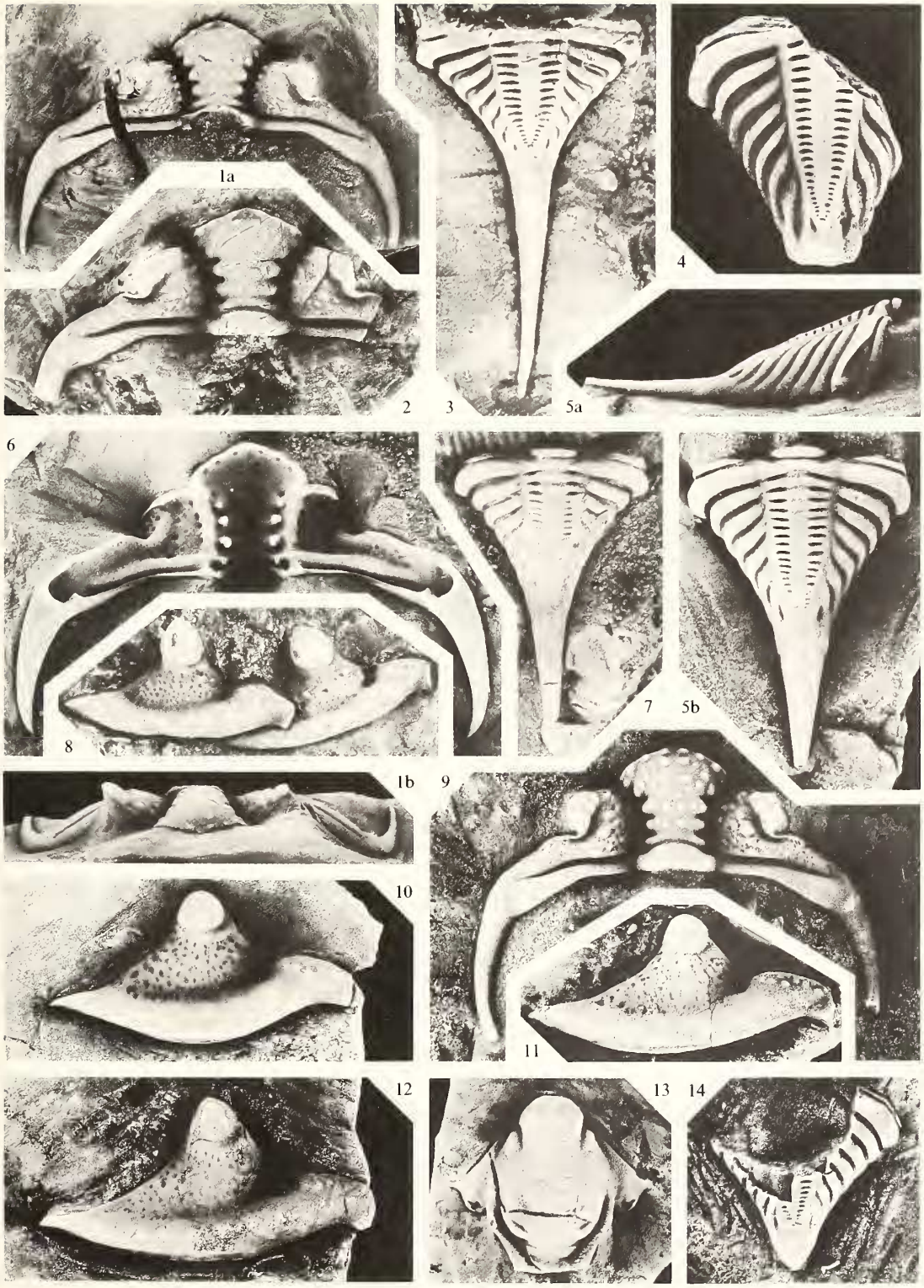
Diagnosis. Cranidium very wide, short. Glabella only weakly convex, depressed posteriorly. Rachial furrows wide. 1L well developed, non-tuberculate. Eyes very low. Genal spines very stout and long. Glabella lacking tubercle row VI, eight tubercles on anterior border, PL set far from margin. Free cheek with faint tuberculation, border furrow shallow. Pygidium with sixteen to twenty-four rachial rings, pleural tips poorly defined on lateral margin. R/P ratio 1·7–2·2. Mucro at least as long as rachis. All tuberculation of low relief.

Description. Cranidium with width to sagittal length 3·3:1–3·5:1. Faint sagittal depression present. 1S and 2S can be traced across glabella as very faint depressions. Tubercles on fixed cheek along rachial furrow small, arrangement opposite lateral glabellar lobes indistinct. The six central tubercles on anterior cranidial border set in contact with margin, PL set more posteriorly. Tubercle row I sometimes absent (Pl. 46, fig. 9). Fixed cheek between palpebral lobe and rachial furrow wide (tr.), densely tuberculated and pitted. Genal spines at least as long as glabella. Free cheek subtriangular, lateral margin only gently convex, border furrow meeting anterior branch of facial suture at about midlength. Border faintly granular (Pl. 46, fig. 10). Rostral suture short, as long as height of visual surface. Rostral plate unknown. Labral plate (Pl. 45, figs. ?12, ?14, ?15; Pl. 46, fig. 13) similar to *E.* (*E.*) *iutersitus* sp. nov., with rhynchos rounded or truncated (this may be abnormal) anteriorly.

Thorax of eleven segments. Stout axial spine on tenth segment. Presence of axial spines or tubercles anterior to this not known. Pygidium with evenly curved lateral margin, with very weak bulges of pleural tips. Pleural

EXPLANATION OF PLATE 46

Figs. 1–14. *Encrinurus* (*Encrinurus*) *stubblefieldi* Tripp, 1962. All Hemse Marl SE. Alva kanal (10), Botvide 1 (9), Gannor 3 (2, 4, 11–14), Hulte 3 (5), Klasård 1 (3), Vaktård 2 (8), Västlaus 1 (7), unknown locality no. 1 (1, 6). 1*a*, *b*, Ar52468, dorsal and anterior views of cranidium, ×2. 2, Ar51774, dorsal view of incomplete cranidium, ×2·5. 3 and 4, dorsal view of pygidium. 3, SGU 5053, ×5 (coll. C. Bergman 1984). 4, Ar52470, incomplete, ×3. 5*a*, *b*, Ar52469, lateral and dorsal views of pygidium, ×4. 6. Ar52471, ventral view of cranidium, ×3. 7, Ar51771, dorsal view of pygidium, ×4 (coll. G. Holm 1904). 8, SGU 5054–5055, exterior view of two small free cheeks, ×5 (coll. S. Laufeld 1984). 9, Ar51782, dorsal view of small cranidium, ×4. 10–12, exterior view of free cheek. 10, Ar30566, ×3 (coll. G. Lindström). 11, Ar51778, ×3. 12, Ar51775, ×3. 13, Ar51776, exterior view of labral plate, ×3 (truncated rhynchos abnormal?). 14, Ar51783, dorsal view of incomplete pygidium, mucro short, abnormal, ×3.



RAMSKÖLD, *Encrinurus* (*Encrinurus*) *stubblefieldi*

furrows often with both rib furrow and interpleural furrow distinct. Mucro about twice as wide (tr.) as thick (dorsoventrally) at base. About three faint axial tubercles.

Discussion. All British specimens examined are moulds, but distinctive enough to allow the Gotland material to be assigned to *stubblefieldi* without doubt. The testiferous specimens described by Schrank (1972) from German Ludlow erratics are indistinguishable from Gotland material.

E. (*E.*) *stubblefieldi* is also present in the Podolian Ludlow. Specimens kindly lent by Dr R. M. Owens can be confidently assigned to *stubblefieldi*. The material is from the Grinchuk Suite of the Malinovtsy Horizon, localities 6 and 7 of the stratigraphical excursion in Tsegelnyuk *et al.* (1983) (see also *Balizoma obtusus* below). The Podolian Přídolí pygidium figured by Balashova (1968*a*) as *E. stubblefieldi* lacks a sagittal band, and is not closely related to *stubblefieldi*, or to *E.* (*E.*) *uasutus* sp. nov. (= *E.* cf. *punctatus* sp. 3 of Schrank 1972, who referred Balashova's specimen to that taxon).

E. (*E.*) *intersitus* sp. nov. resembles *E.* (*E.*) *stubblefieldi* in several features. These include the wide cephalon, strong 1L, glabellar shape, laterally set eyes, stout genal spines, very similar labral plate, long axial spine on the tenth thoracic segment, long mucro, and low R/P ratio. The shape of the free cheek and the tuberculation is, however, very different. The pattern of distribution (see text-fig. 9 and 'Remarks on distribution'), together with the morphological similarities, suggest that *stubblefieldi* may be directly related to *intersitus*. No other described species appears to be closely related to *stubblefieldi*.

Encrinurus (*Encrinurus*) sp. A.

Plate 47, figs. 1, 2, 5, ?7; text-fig. 7

Material and localities. All specimens are from the Slite Beds, Slite Marl, undifferentiated but close to the transition Slite Marl/unit g. Boge parish—Mojner 3 (Ar52277–52279); Endre parish—Bolarve 1 (Ar51949), Hajdungs 1 (SGU 5051 and unnumbered SGU material); Follingbo parish—Follingbo 6 (Ar52494). In total ten pygidia and possibly one free cheek.

Description. The material differs from *E.* (*E.*) *punctatus* Form C in the following features: pygidial rachis wider, lateral margin almost straight in dorsal view; in lateral view curved upward at the sixth and seventh segments, base of mucro at a level above pygidial margin. Mucro circular in section, length unknown but at least half the length of rachis. R/P ratio 2·1–2·2. Doublure narrow. The free cheek possibly belonging to this species (Pl. 47, fig. 7) has a highly stalked eye and a precranidial lobe with sparse, very large tubercles. Large pygidia give an estimated total length for an extended exoskeleton of just over 70 mm.

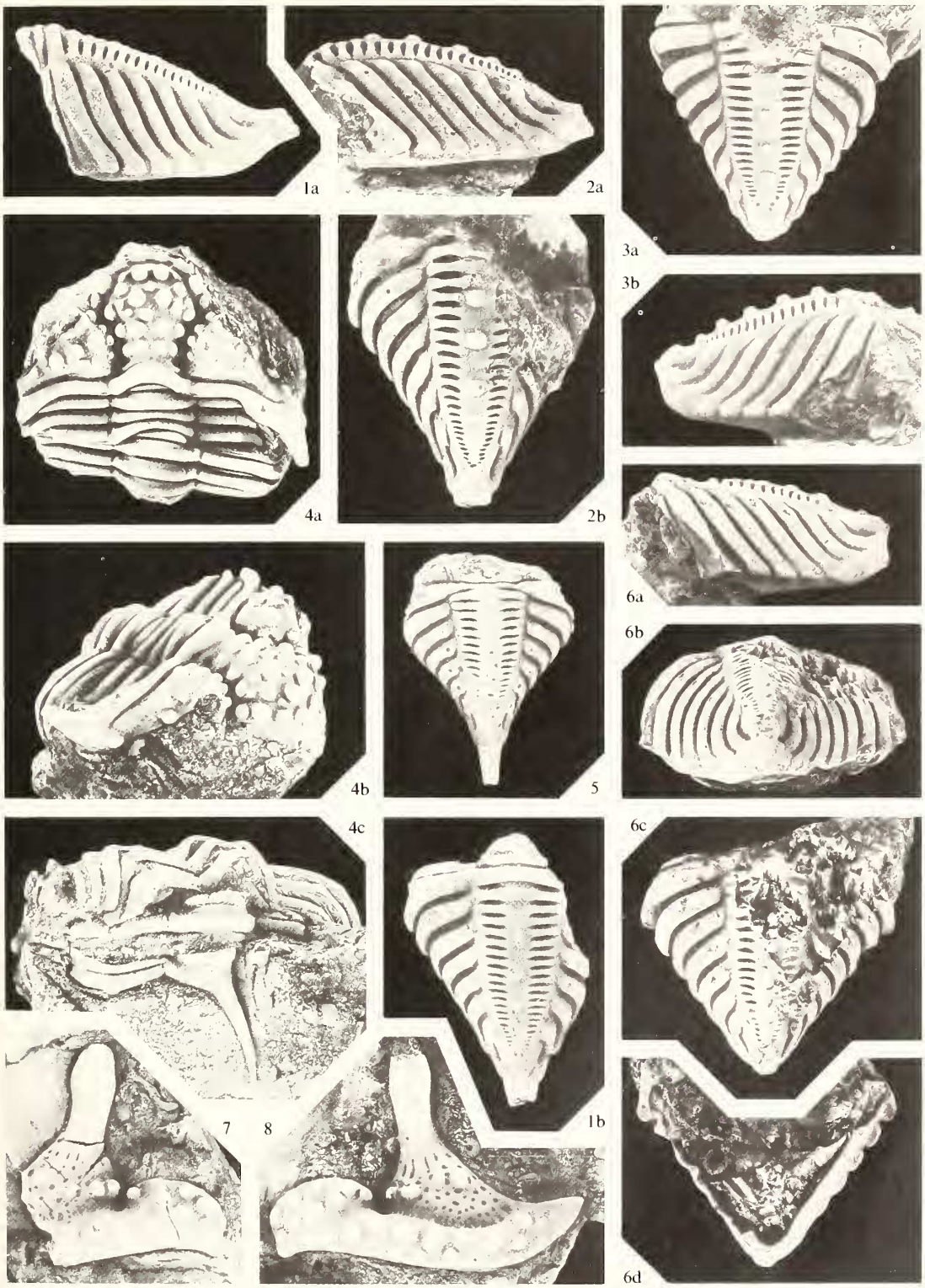
Discussion. This form occurs together with *E.* (*E.*) *punctatus* Form C at all the above localities, in proportions from 1:1 to 1:10. Although dimorphism has been proposed for a related species, *E.* (*E.*) *egani* Miller, 1880, this seems unlikely here. First, *E.* (*E.*) *punctatus* Form A and Form B are both monomorphic; secondly, *E.* (*E.*) sp. B is likely to be derived from *E.* (*E.*) sp. A, and the two forms appear to be a short side-branch from *E.* (*E.*) *punctatus*.

EXPLANATION OF PLATE 47

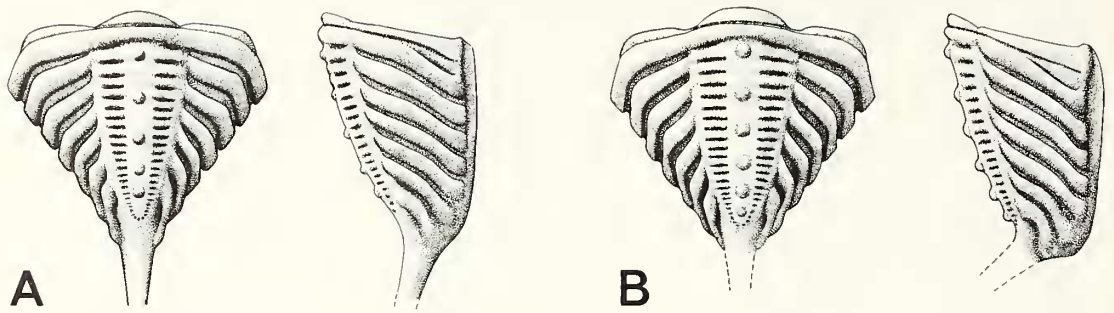
Figs. 1, 2, 5, ?7. *Encrinurus* (*Encrinurus*) sp. A. All Slite Beds, Slite Marl. Bolarve 1 (2), Hajdungs 1 (5), Mojner 3 (1, 7). 1 and 2, lateral and dorsal views of pygidium. 1*a*, *b*, Ar52279, ×5. 2*a*, *b*, Ar51949, ×2. 5, SGU 5051, dorsal view of pygidium, ×3 (coll. G. Liljevall 1908). 7. Ar52277, exterior view of incomplete free cheek, ×3.

Figs. 3, 6, ?8. *E.* (*E.*) sp. B. All Slite Beds, ?Slite Marl/unit g. Slitebrottet 2 (8), Slite 'a' c (3), unknown locality (6). 3*a*, *b*, Ar30749, dorsal and lateral views of pygidium, ×3. 6*a–d*, Ar30713, lateral, posterior, dorsal, and ventral views of pygidium, ×2.5. 8, Ar52276, exterior view of free cheek lacking visual surface, ×2·5 (coll. Amelang 1983).

Fig. 4*a–c*. *E.* (*E.*) sp. C. Ar51788, incomplete, partly disarticulated, enrolled specimen, Urgude 3, Hemse Marl NW; dorsal, oblique anterolateral, and exterior views, note thoracic axial spine, ×2·5.



RAMSKÖLD, *Encrinurus* (*Encrinurus*)



TEXT-FIG. 7. A, B, dorsal and lateral views of reconstructed pygidia. A, *Encrinurus* (*Encrinurus*) sp. A (based mainly on Ar52279), ×4. B, *E.* (*E.*) sp. B (based mainly on Ar30713 and Ar30749), ×3.

E. (*E.*) sp. A closely resembles the American Wenlock *E.* (*E.*) *egani* Miller, 1880, redescribed by Holloway (1980). Similarities include the highly stalked eye and the long mucro with its base raised dorsally. However, *E.* (*E.*) sp. A is known too incompletely to be compared accurately with *egani*.

Encrinurus (*Encrinurus*) sp. B

Plate 47, figs. 3, 6, ?8; text-fig. 7

Material and localities. All specimens are from the Slite Beds, probably unit g, but possibly Slite Marl near the transition to unit g. Othem parish—slite 'a' c (Ar30749–30750); unknown locality (Ar30713). A free cheek (Ar52276), from Slitebrottet 2, Othem parish, possibly belongs to this species.

Description. The three pygidia differ from *E.* (*E.*) sp. A mainly in having the base of the mucro set high above the level of the lateral pygidial margin. The seventh pleural pair is curved backwards to a horizontal position. The mucro itself is not preserved, but from its base it is clear that it must have been directed upwards at 45° or more. R/P ratio 2·1–2·2. The ventral part of the border (Pl. 47, fig. 6*d*) is very narrow. The free cheek probably belonging to this species (Pl. 47, fig. 8) has a very highly stalked eye.

Discussion. This species is probably slightly younger than *E.* (*E.*) sp. A; the occurrence in unit g of the Slite Beds is suggested by the stylolitic structures in one pygidium (Pl. 47, fig. 6); such structures are common in unit g but rare in the Slite Marl in this area. The material shows a further development of the characteristic features of *E.* (*E.*) sp. A; the raised mucro and the highly stalked eye. It is likely that *E.* (*E.*) sp. B is a direct descendant from *E.* (*E.*) sp. A, but since both species are so incompletely known, new material must be collected to confirm this suggestion. *E.* (*E.*) sp. B is not as close to *E.* (*E.*) *egani* Miller, 1880 as *E.* (*E.*) sp. A (see discussion of the latter species), but the three species are more similar to each other than to any other *Encrinurus*, with the possible exception of *E.* (*E.*) *odvaldensis* sp. nov. Highly stalked eyes are common in trilobites, though unusual in *Encrinurus* outside the above group. A mucro directed upwards is not otherwise known in *Encrinurus*, but is present in some Phacopida, e.g. *Chattiaspis* (see Hammann 1974, pl. 7, fig. 107*b*).

Encrinurus (*Encrinurus*) sp. C

Plate 45, figs. ?10 and ?11; Plate 47, fig. 4

Material and localities. Ar51788, cranidium with ten thoracic segments, from Urgude 3, Sproge parish, Hemse Beds, Hemse Marl NW. Two more specimens (Ar52280, free cheek; Ar52282, almost complete exoskeleton) from Urgude 4 are assigned questionably.

Description. Differs from *E.* (*E.*) *macrourus* in the following features: cranidial tubercles very large, anterior tubercles higher than wide. Eight tubercles on anterior cranidial border. Tubercle pair VI-1 absent. Tubercle

iv-0 instead of tubercle pair iv-1. Seventh thoracic segment broken axially indicating axial spine, on tenth segment is a very long, stout spine; both segments with a tubercle above fulcrum (Pl. 47, fig. 4*c*). Additional differences in the two questionably assigned specimens are: eyes high, with stalk (on free cheek) over 1·5 times height of visual surface (Pl. 45, fig. 11); pygidium with broken mucro circular in section, possibly indicating long mucro.

Discussion. These specimens represent a fundamental taxonomic problem. If the two questionably assigned specimens were the only known they would, perhaps questionably, be referred to *E.* (*E.*) *macrourus*, which is common at both Urgude 3 and 4. However, the third specimen differs more from *macrourus* than most species within *E.* (*Encrinurus*) differ from each other, and the two first specimens are definitely closer to this specimen than to *macrourus*. The possibility that the specimens are extreme, but not abnormal, variations within *macrourus*, cannot be excluded, but if this view is followed in encrinurid taxonomy, very few species can be defined accurately. At least until new material shows otherwise, *E.* (*E.*) sp. C is regarded as an independent species. No described *Encrinurus* is particularly close to *E.* (*E.*) sp. C, but some features (stalked eyes, long mucro?) are shared with *E.* (*E.*) spp. A and B of this paper.

Subgenus Encrinurus (australurus) subgen. nov.

Name. Latin *australis*, southern, and Greek *oura*, tail; referring to the numerous Australian species included.

Type species. E. mitchelli Foerste, 1888, from the Yarwood Siltstone Member of the Black Bog Shale (Leintwardinian; Strusz 1980, p. 24), Yass Basin, New South Wales, and Coppins Crossing, Canberra, Australia.

Other species. See Strusz 1980, p. 20 (*E. mitchelli* species-group).

Diagnosis. 1L well developed, only slightly smaller than 2L–4L. 1S separate from occipital furrow. Preglabellar furrow always present but usually faint. Anterior border of cranidium with ten to eighteen tubercles, usually about fourteen. Four large tubercles on fixed cheek along rachial furrow. Eyes low, never stalked. Genal angles rounded or angular, never with spine. Labral plate with short posterior border. No thoracic spines. Pygidium large for genus, non-mucronate, with narrow rachis and 10^2–15^1 pleurae.

Remarks. This group was discussed comprehensively by Strusz (1980), and although he did not recognize it as a distinct subgenus of *Encrinurus*, his definition and discussion cover all important aspects of *E.* (*Australurus*). This subgenus is geographically restricted to Australia, south-east Asia, and Japan. One species is upper Llandovery in age, the remainder are Wenlock and Ludlow. *E.* (*Australurus*) is compared with *E.* (*Nucleurus*) subgen. nov. under the latter.

Subgenus encrinurus (nucleurus) subgen. nov.

Name. Latin *nucleus*, core, and Greek *oura*, tail; referring to the central morphological position of this subgenus.

Type species. E. abyssalis Männil, 1977 from the Kolka core, northwestern Latvia, Raikküla Stage (middle Llandovery); known also from Gustavsvik near Motala, Östergötland, south central Sweden, Klubbudden Stage (middle–upper Llandovery).

Other species. E. anticostiensis Twenhofel, 1928; *E. diabolus* Tripp *et al.*, 1977; *E. elegantulus* Billings, 1866; *E. inexpectatus* Šnajdr, 1978; *E. kiltsiensis* Rosenstein, 1941; *E. mareki* Šnajdr, 1975; *E. mullochensis* Reed, 1931; *E. palmrei* Männil, 1958; *E. rotundus* Männil, 1977; *E. rumbaensis* Rosenstein, 1941; *E. selistensis* Männil, 1977. These species are all Llandovery in age. The poorly known *E. hypoleprus* Stearn, 1956 and *E. nereus* Hall, 1867 (both Wenlock) show similarities to the above group (i.a. in the R/P ratio), and are questionably assigned to *E.* (*Nucleurus*).

Diagnosis. Glabella relatively short and wide. Anterior cranidial border with nine to fourteen tubercles, usually 10–12. Tubercles on fixed cheek along rachial furrow equal in size or slightly larger than other fixed cheek tubercles. 1L usually small, ridge-shaped, set well below 2L, never tuberculate abaxially. Genal angle rounded or with a tiny spine. Labral plate with wide rhynchos

not reaching level anteriorly with labral suture, posterior border of small to medium length. No thoracic axial spines. Pygidium short and wide, non-mucronate. 7^2–10^1 pleural ribs. Posterior pleurae commonly merged to form a 'loop'. R/P ratio 1·8–2·5.

Discussion. Most of the species assigned to *E.* (*Nucleurus*) were referred to *Fragiscutum* by Holloway (1980). Although there are certain similarities, especially in the pygidium, *Fragiscutum* is very different in the cephalon, particulary in the free cheek, and has only ten thoracic segments. The differences are regarded here as fundamental, and *Fragiscutum* is restricted to *F. rhytium* and *F. glebalis*. It is, however, not unlikely that *E.* (*Nucleurus*) gave rise to *Fragiscutum*, or at least that the two groups share a common ancestry around the Ordovician/Silurian boundary.

E. (*Nucleurus*) differs from *E.* (*Encrinurus*) mainly in consisting of non-mucronate species with a rather short, wide glabella, a short rhynchos and a wide, short pygidium. The subgenus is distinguished from *E.* (*Australurus*) mainly by the small 1L, the wide and short rather than elongated pygidium, and the 7^2–10^1 pleurae compared to 10^2–15^1. There is practically no overlap in time between the two subgenera, and they are completely separated geographically. It is therefore, at least at present, difficult to determine their relation to each other. Only the type species of this subgenus is known from Sweden, *E.* (*Nucleurus*) *abyssalis* Männil, 1977; this will be described by Ramsköld and Bassett (in prep.).

Genus BALIZOMA Holloway, 1980

Type species. Calymene variolaris Brongniart, 1822, from the Much Wenlock Limestone Formation (upper Wenlock) and lower Ludlow, Dudley, West Midlands, England; by original designation.

Other species. E. hyperboreus Thomas *in* Thomas and Narbonne, 1979; *E. indianensis* Kindle and Breger, 1904; *Cryptonymus obtusus* Angelin, 1851 (including the junior subjective synonym *E. obtusus erraticus* Schrank, 1972, and the possible synonyms *E. dimitrovi* Perry and Chatterton, 1979, *E. rosensteinae* Tripp *et al.*, 1977, and *Balizoma dakon* Šnajdr, 1983); *E.* sp. of Tripp *et al.* 1977; *B.* sp. of Holloway 1980; *E.* aff. *hyperboreus* of Thomas *in* Thomas and Narbonne, 1979 (cranidium and free cheek only, the pygidium may belong to *Frammia*), and *E.* sp. cf. *E.* (*Frammia*) *arcticus* of Bolton 1965. *Cromus transiens* Barrande, 1852 (see von Gaertner 1930*a*, pl. 25, figs. 9–10) has been studied from Bohemian material in British collections; this material belongs to *Balizoma*. *E. subvariolaris* Münster, 1840 (see von Gaertner 1930*a*, pl. 25, fig. 6) probably also belongs to *Balizoma*. *E.* spp. F and G of Lane (1979) are poorly known but show certain similarities to *Balizoma*.

Diagnosis. Tubercles ii-1, II-0_R, 1, iii-0 form a pentagon with tubercle II-0_R, when present, in centre. Tubercles on 2L, 3L, 4L, and PL commonly displaced adaxially. Anterior border of cranidium with ten to twelve tubercles. Genal angle typically rounded, tiny spine may be present. Field of cheek thickly covered with tubercles. Pygidium with seven to fifteen rings and six to twelve pleurae; one to two fewer pleurae than rings, R/P ratio 1·1–1·4. Sagittal groove present, rachial rings commonly with a pair of tubercles flanking the groove, several axial tubercles. Tip non-mucronate, rounded in both dorsal and lateral views.

Discussion. In addition to the diagnostic features listed above, all except the type species have non-stalked eyes and a very low field of free cheek. Some cephalic features considered diagnostic for *Balizoma* by Holloway (1980) are also found in other taxa within the '*variolaris* plexus' (of Strusz 1980), e.g. in *Fragiscutum* Whittington and Campbell, 1967, so the diagnostic emphasis must be on pygidial features, as also noted by Holloway. A very useful criterion is the R/P ratio (defined under 'Notes on morphology' above) of 1·1–1·4, but no single feature is completely restricted to *Balizoma*, which is therefore distinguished by the unique combination of characters.

Thomas (1981, p. 64) preferred not to use *Balizoma* although 'accepting that generic status may eventually be justified', while Šnajdr (1983) recognized the genus and assigned certain Bohemian species to it. *Balizoma* is conceived here in a more restricted sense than by either Holloway or Šnajdr. Species assigned by them to *Balizoma* but excluded here are: *E. inexpectatus* Šnajdr, 1978;

E. mareki Šnajdr, 1975; *E. nereus* Hall, 1867; *E. subvariolaris concomitans* Přibyl and Vaněk, 1962; *E. testosteron* Šnajdr, 1981; and *E. tuberculifrons* Weller, 1907. All these species have a much higher R/P ratio than *Balizoma*. The very similar Bohemian Přídolí *concomitans* and *testosteron* may be derived from *Balizoma*, but they also show similarities to Fragiscutum, and their position is uncertain. The American Wenlock species *nereus* and *tuberculifrons* are both in need of revision. *E. tuberculifrons* was referred hesitantly to *Encrinuroides* by Strusz (1980); photographs of the type specimens support that view. *Encrinurus nereus* seems to be close to the large group of middle and upper Llandovery species within the '*variolaris* plexus' here formalized into *E.* (*Nucleurus*) subgen. nov. *Balizoma* and *Fragiscutum* are apparently related closely to *E.* (*Nucleurus*) and could have their origins in lower Llandovery species similar to *E. rotundus* Männil, 1977, the earliest of the species assigned to *E.* (*Nucleurus*). That species and several others here included in *E.* (*Nucleurus*) were referred to *Fragiscutum* by Holloway (1980). There are certainly similarities, but at present it seems best to restrict *Fragiscutum* to *F. rhytium* Whittington and Campbell, 1967 and *F. glebalis* Campbell, 1967 (see discussion of *E.* (*Nucleurus*) above. The late Llandovery-early Wenlock *Perryus* Gass and Mikulic, 1982, including *P. severnensis* Gass and Mikulic, 1982 (= *E.* sp. 1 of Norford 1981) and possibly *E. globosus* Makisimova, 1962, is more distantly related to the other species discussed above, but may be closer to the '*variolaris* plexus' than to the *Encrinuroides/Cromus* line which was suggested by Gass and Mikulic (1982). Two members of the '*variolaris* plexus' are known from Sweden: *B. obtusus* (Angelin, 1851) from Gotland, and *E.* (*Nucleurus*) *abyssalis* Männil, 1977 from Östergötland (will be described in Ramsköld and Bassett (in prep.)).

Balizoma obtusus (Angelin, 1851)

Plate 40, fig. 2; Plate 48, figs. 1–14; Plate 49, figs. 1–10

* 1851 *Cryptonymus obtusus* Angelin, p. 3, pl. 4, fig. 9.
v *non* 1901 *Encrinurus obtusus*; Lindström, p. 56, pl. 4, figs. 14 and 15 [= *E.* (*E.*) *intersitus* sp. nov. or *E.* (*E.*) *stubblefieldi* Tripp, 1962].
v. 1972 *Eucrinurus* (*Frammia*) *o. obtusus* (Angelin, 1851); Schrank, p. 45, pl. 13, fig. 3 [with synonymy list].
. 1972 *Ecrinurus* (*Frammia*) *obtusus erraticus* Schrank, p. 45, pl. 13, figs. 4–7; pl. 14, figs. 1–5 [with synonymy list].
. 1972 *Eucrinurus* cf. *punctatus* 3; Schrank, pl. 11, fig. 8, *non* figs. 9 and 10; pl. 12, figs. 1–3 [= *E.* (*E.*) *nasutus* sp. nov.].
v? 1977 *Encrinurus rosensteinae* Tripp *et al.*, p. 860, pl. 15, figs. 1–13; text-fig. 3c.
? 1979 *Eucriurus dimitrovi* Perry and Chatterton, p. 589, pl. 72, figs. 1–3; pl. 73, figs. 1–17, 29–31; pl. 74, figs. 1–14, 18–23, 30–35 [with synonymy list].
? 1983 *Balizoma dakon* Šnajdr, p. 175, pl. 1, fig. 2.

Neotype. Ar30309, almost complete exoskeleton from Hässle, Östergarn parish, Hemse Beds, unit c (or d), selected and figured by Schrank 1972, pl. 13, fig. 3–3*b*.

Additional material. See under each form and 'Discussion' below.

Diagnosis. Anterior border of cranidium with ten to twelve tubercles. 1L non-tuberculate. One or two tubercles between palpebral lobe and axial furrow. Field of free cheek with seven to thirteen tubercles. Pygidium with width to length 1·2 : 1–1·6 : 1. Ten to fourteen axial rings, 8^2–11^2 pleurae. Axial tuberculation varying from tubercles on most rings to on about every second.

Remarks. The three slightly different Gotland forms are treated here as one species and are diagnosed as such. The resulting diagnosis is not precise enough to separate *obtusus* from *dimitrovi*, *rosensteinae*, and *dakon*, and the possible synonymy of these species with *obtusus* is discussed below.

Description. Form A; the 'type form'. Restricted to the northeastern limestone areas in the Hemse Beds, and the Eke Beds outlier at Lau Backar. The neotype is from the Östergarn area, Angelin's type locality, where only Form A is found.

Material and localities. Five nearly complete exoskeletons, five free cheeks, and over thirty pygidia (all from Hemse Beds), plus two glabellae, one free cheek, and about ten pygidia from Lau Backar 1. Hemse Beds, unit b or c: Östergarn parish—ditch 1 km north-west of Katthammarsvik (probably = Ängmans 1). Hemse Beds, units c and d: Ardre parish—Botvalde, Kaupungs 3, Rudvier 1; Kräklingbo parish—field east of road 200 m north of Österby; Östergarn parish—Brännklint, Grogarnshuvud 1, Gutenviks 1, Hammarudden 1, Kuppen, Kyrkberget, ditch at Herrvik. Hemse Beds, upper part: Gammelgarn parish—Herrgårdsklint 1, Millklint (or Torsburgen). Eke Beds, upper part: Lau parish—Lau Backar 1. A few poorly preserved specimens from the following more southwesterly localities may also belong to Form A: Garde parish—large ditch 1 km south-east of Garde church. Lye parish—Mannegårda. Fardhem parish—Sandarve kulle (all Hemse Beds, upper part).

Comparative description. Density and number of glabellar tubercles variable (compare Pl. 48, fig. 3 with Schrank 1972, pl. 13, fig. 3). Eye small, occupying less than half the length (exsag.) of field of cheek (Pl. 48, fig. 6*a*). Part of fixed cheek between posterior border furrow and posterior branch of facial suture as wide as or wider (exsag.) than posterior border. Field of free cheek with eight to thirteen tubercles. Lateral border furrow meets posterior branch of facial suture closer to margin than to eye. Genal angle with tiny spine in small specimens, rounded in larger ones. Posterior borders and occipital ring each with several faint, perforate tubercles (Pl. 48, fig. 4); all thoracic segments with perforations in corresponding places. Pygidium with width to length 1·3–1·4 : 1, 10^1–11^1 pleurae, rarely up to 12^1. Eleven to fourteen rachial rings, usually thirteen recognizable, occasionally there is a terminal piece composed of several 'segments' (Pl. 48, fig. 9*c*). Pleural regions high dorsoventrally (see posterior views Pl. 48). Dorsoposterior part evenly sloping in lateral view, posteriormost point usually well below last rachial ring. Posteriormost paired pleural furrows form a three-quarter circle open upwards, not reaching pygidial margin (Pl. 48, figs. 2*b*, 7*b*, 8*b*, 9*b*, 10*b*). Pleurae rather flat-topped, the plane formed by each ridge only slightly inclined to give a very weak imbricating appearance of the pleural areas. Pleural furrows usually very narrow. Axial tuberculation very variable, from a distinct tubercle on most rings to tubercles on about every second ring starting from fourth or fifth ring; there are commonly small, faint tubercles also on many 'blank' rings. Rachial rings and pleurae with faint tubercles or perforations in corresponding positions to those on thorax.

Form B. Restricted to the 'marl' west and south of the southwestern outcrops of the Hemse Beds limestone area.

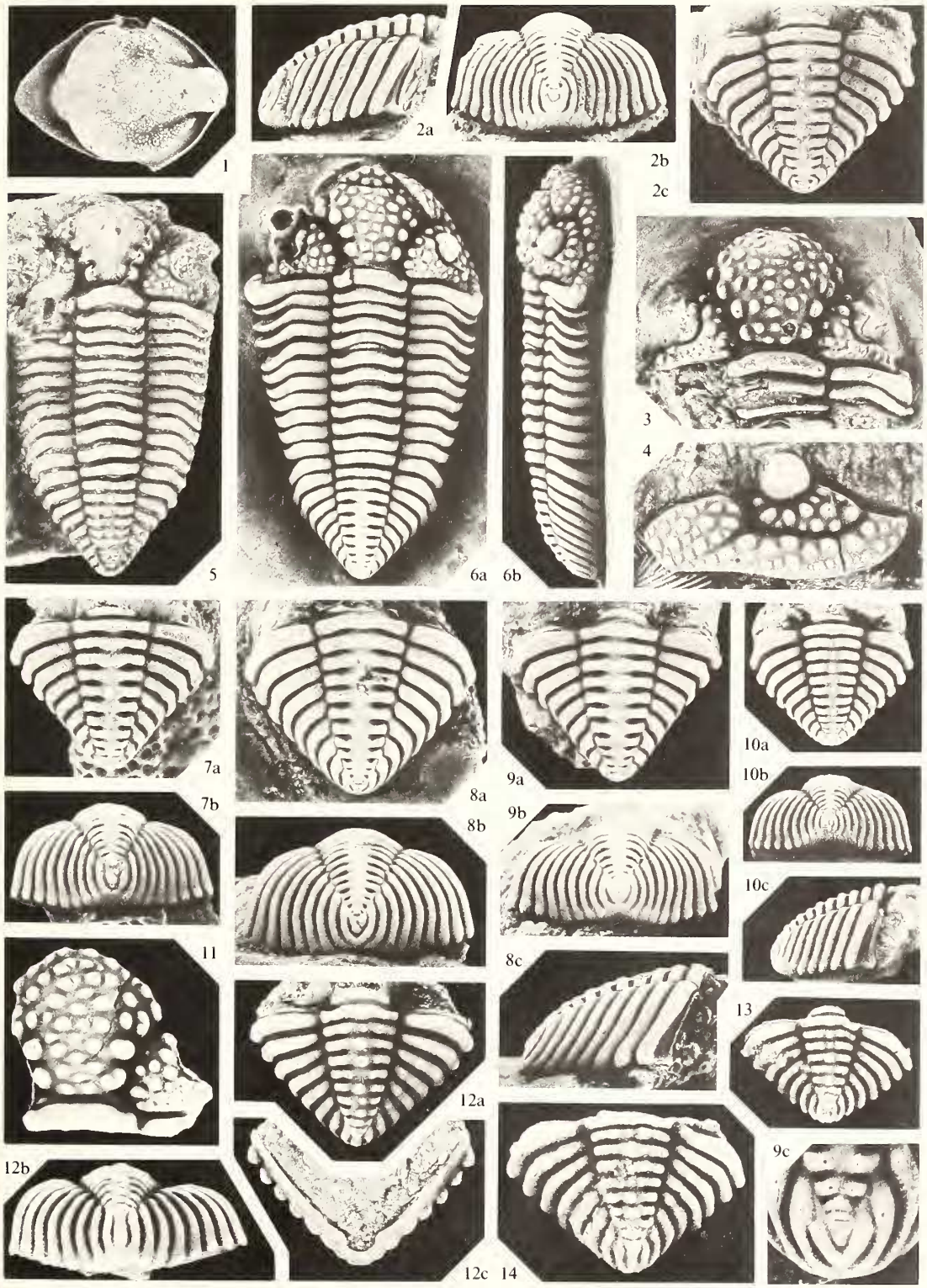
Material and localities. Two nearly complete exoskeletons, two complete and four incomplete cranidia, four free cheeks, and about fifty pygidia. Klinteberg Beds, Klinteberg Marl: Gerum parish—Ajmunde 1. Hemse Beds, Hemse Marl NW: Fardhem parish—Gardarve 1, Gerete 1, Burge sawmill; Hablingbo parish—Lilla Hallvards 5; Hemse parish—east of road south-east of Niksarve (in Fardhem parish); Silte parish—Mästermyr 1, Smissarve 1. Hemse Marl SE: Burs parish—Rone drainage ditch at Västlaus (probably = Västlaus 1); Hemse parish—Hulte 3, Hemse church. Two pygidia from Loggarve 2 (Klinte parish, Mulde Beds, uppermost part) apparently belong to Form B; this stratigraphically aberrant occurrence is discussed under 'Remarks on distribution' below.

EXPLANATION OF PLATE 48

Figs. 1 and 11. *Balizoma obtusus* (Angelin, 1851) Form A (or C?). Both from upper Eke Beds, Lau Backar 1. 1, Ar52346, exterior view of labral plate, ×6. 11, Ar52345, dorsal view of incomplete cranidium, ×4.

Figs. 2–10. *B. obtusus* (Angelin, 1851) Form A. Hemse Beds, unit c (2, 3, ?4, 5, ?6, ?8, 10), Eke Beds, upper part (7, 9). Brännklint (5), Lau Backar 1 (7, 9), 'Östergarn' (2, 3, 10), ditch 1 km north-west of Katthammarsvik (4, 8), unknown locality (6). 2*a–c*, Ar30356, lateral, posterior, and dorsal views of pygidium, ×3. 3, Ar30359, dorsal view of cranidium of almost complete specimen, (note rudimentary genal 'spine'), ×4. 4, Ar51772, exterior view of free cheek, ×5. 5, Ar30352, dorsal view of fairly complete specimen, ×4 (coll. G. Lindström). 6*a*, *b*, Ar52344, dorsal and lateral views of complete exoskeleton ×4. 7*a*, *b*, Ar51768, dorsal and posterior views of pygidium ×5. 8*a–c*, Ar51773, dorsal, posterior, and lateral views of pygidium, ×4. 9*a–c*, Ar51767, dorsal and posterior views and detail of rachis of pygidium, *a*, *b*, ×4, *c*, ×12. 10*a–c*, Ar30339, dorsal, posterior, and lateral views of pygidium, ×5.

Figs. 12–14. *B. obtusus* (Angelin, 1851) Form C. All from upper Eke Beds, Lau Backar 1. 12*a–c*, Ar51768, dorsal, posterior, and ventral views of largest pygidium, ×4. 13 and 14, dorsal view of pygidium. 13, Ar52347, ×6. 14, Ar52348, ×6.



RAMSKÖLD, *Balizoma obtusus*

Comparative description. Glabella similar to Form A. Eye of two types; either small (similar to Form A) or large (see 'Discussion' below). Part of fixed cheek between posterior border furrow and posterior branch of facial suture usually narrower (exsag.) than posterior border. Field of free cheek with seven to eleven tubercles (Pl. 49, figs. 2 and 7). Lateral border furrow meets posterior branch of facial suture closer to eye than to margin. Tubercles and perforations on occipital ring and posterior border as in Form A. Pygidium with width to length 1·2–1·4 : 1. Usually 10^1 pleurae (51 %), range 9^1–10^2. Ten to eleven rachial rings, one large specimen has twelve rings. Pleural regions lower than in Form A; most specimens are, however, slightly distorted. Dorsoposterior part in lateral view commonly angular and bent down just posterior to the last rachial ring, posteriormost point commonly at this flexure, overhanging postrachial pleural region. Posteriormost paired pleural furrows as in Form A. The plane formed by the outer surface of each pleural rib is strongly inclined anteroventrally from the general surface plane of the pygidium. Pleural furrows fairly wide. Axial tubercles on every second ring on average, commonly starting on fourth ring. Weak tubercles and perforations present on rachial rings and pleurae at least to some extent.

Form C. Only known from pygidia from the upper Eke Beds at Lau Backar 1, Lau parish, where Form A is also found (more commonly). About five pygidia, of smaller size than most of Form A and Form B. A very small incomplete, enrolled specimen possibly belongs to Form C. Two glabellae, one free cheek, and two labral plates from Lau Backar 1 are assigned to Form A, but the possibility that the two forms found together have similar cephala cannot be excluded, and these specimens may belong to either one of the forms.

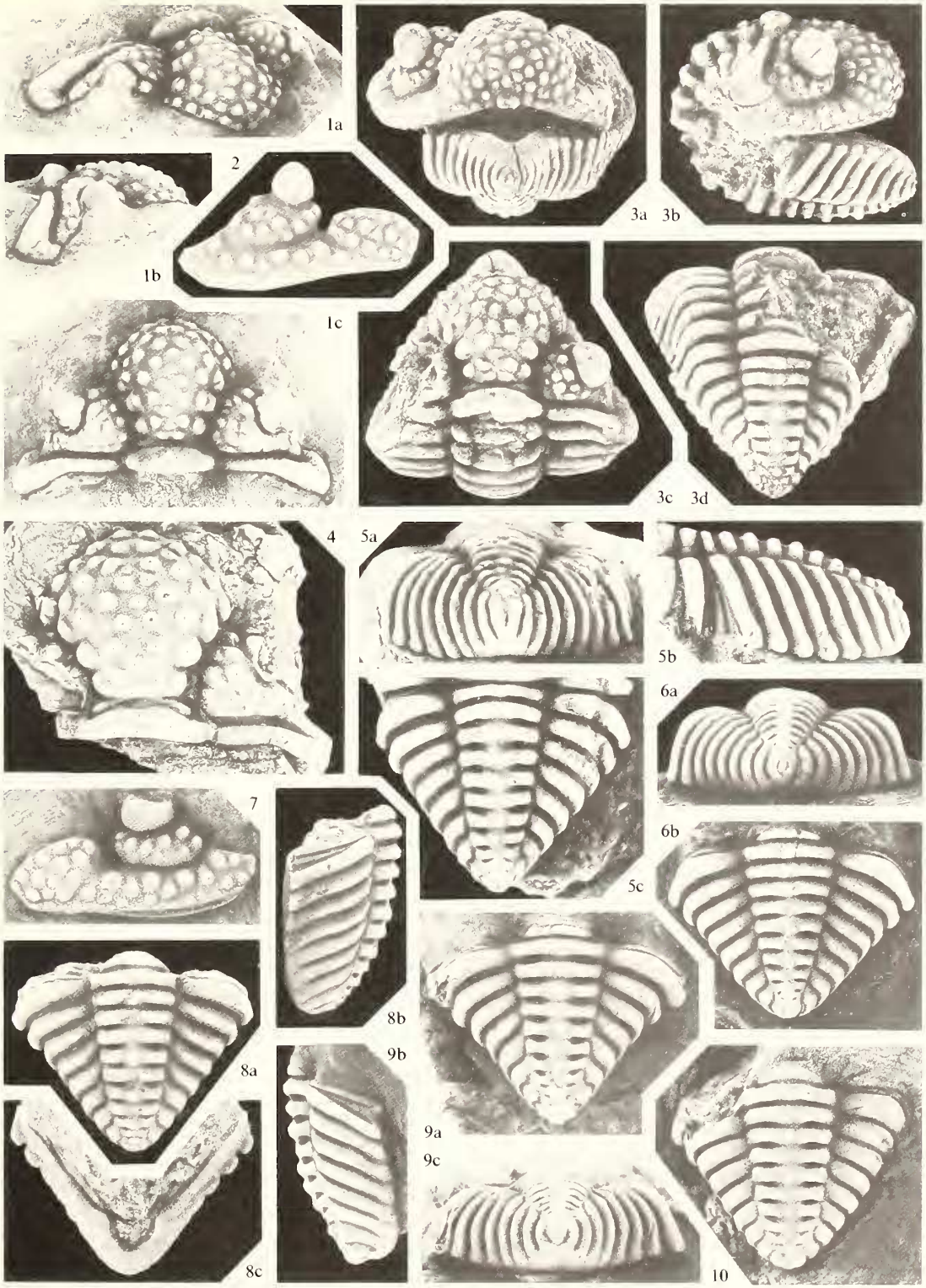
Comparative description. Pygidium with width to length 1·6 : 1, 9^1 pleurae, eleven rachial rings. Pleural regions low dorsoventrally; possibly lower than in Form B, but most specimens are slightly distorted. Dorsoposterior part gently sloping in lateral view, posteriormost point at border flexure. Posteriormost paired pleural furrows subparallel, reaching posterior margin (Pl. 48, fig. 12*b*). Outer surface of each pleura gently convex (exsag.). Pleural furrows wide. Axial tubercles, weak pleural and rachial tubercles, and perforations similar to Form A.

Discussion. It is probably realistic to assume that the three Gotland forms of *B. obtusus* really represent more than one biological species. However, in spite of large samples and excellent preservation, the extensive variation in morphology makes the forms difficult to separate, and Form C is known only from pygidia. Splitting into several species or subspecies is therefore undesirable, at least for the present. Accordingly, the three forms are treated here as morphological forms of *obtusus*, but to avoid loss of information, they are described and figured as separate entities.

Form B is probably slightly older than the Hemse Beds material of Form A, although some overlap in time cannot be ruled out. The differences between the 'limestone' specimens, Form A, and the 'marl' material, Form B, are small but real. Form A specimens are generally better preserved, which may account for part of the differences in pygidial tuberculation, since surface details in Form B are more difficult to observe. However, there are at least two definite differences: 1, the number of pygidial pleurae is clearly different (Table 2). Size has very weak or no correlation with the number of pleurae (text-fig. 8), and the mean size of the two forms is about the same. 2, the pygidial pleural regions have a greater height in Form A, resulting in a more vaulted pygidium than the rather low Form B. The size of the eyes and the field of cheek are also different, but more difficult to evaluate. In Form A the size of the eyes and field of cheek does not vary, while there are

EXPLANATION OF PLATE 49

Figs. 1–10. *Balizoma obtusus* (Angelin, 1851) Form B. Hemse Beds, Hemse Marl NW (2–5, 7), Hemse Marl SE (1, 6, 8–10). Gardarve 1 (2), Hemse church (9), Hulte 3 (1, 6), Mästermyr 1 (4, 5), Västlaus 1 (8, 10), Visne myrs kanal (7), unknown locality (3). 1*a–c*, Ar52335, oblique anterolateral, lateral, and dorsal views of cranidium, ×3. 2, Ar52340, exterior view of free cheek, ×3. 3*a–d*, Ar30381, anterior, lateral, and dorsal views and pygidium of enrolled specimen, ×5. 4, Ar52342, dorsal view of large incomplete cranidium, ×3 (coll. Amelang 1982). 5*a–c*, Ar52343, posterior, lateral, and dorsal views of pygidium of almost complete specimen, ×3 (coll. Amelang 1982). 6*a*, *b*, Ar52337, posterior and dorsal views of pygidium, ×3·5. 7, Ar52338, exterior view of free cheek, ×6. 8*a–c*, Ar31488, dorsal, lateral, and ventral views of pygidium, ×4 (coll. G. Holm 1904). 9*a–c*, Ar30315, dorsal, lateral, and posterior views of pygidium, ×4. 10, Ar51770, dorsal view of pygidium, ×4 (coll. G. Holm 1904).



RAMSKÖLD, *Balizoma obtusus*

TABLE 2. Number of pygidial pleurae in the different forms of *Balizoma obtusus*. The most important localities are listed separately. A two-sided t-test of significance of the mean values has been used to determine differences between certain groups (9^1 is given the value 9, 9^2 = 9·5 etc.). The two Hemse Beds forms (II and IV) give a t = 7·71***, which confirms their dissimilarity in this particular character. Within Form A, Hemse Beds (II) and Eke Beds (III) specimens differ slightly (t = 2·29*), and the Eke Beds material is actually closer to Form B (IV) in this feature (t = 1·70). Within Form B, Hulte 3 specimens commonly have 10^1 pleurae (Pl. 49, fig. 6) and Mästermyr 1 specimens usually have 9^2 (Pl. 49, fig. 5), but this difference is not statistically significant (t = 1·65). The diagram obviously suggests that Form C (VII) is simply one extreme of the variation range of the other Lau Backar 1 material (III). However, this solution seems to be in conflict with other morphological differences, although most of the Form C material is distorted and incomplete, and the evidence is not conclusive. (One, two, and three asterisks indicate significance at the 5 %, 1 %, and 0·1 % level, respectively.)

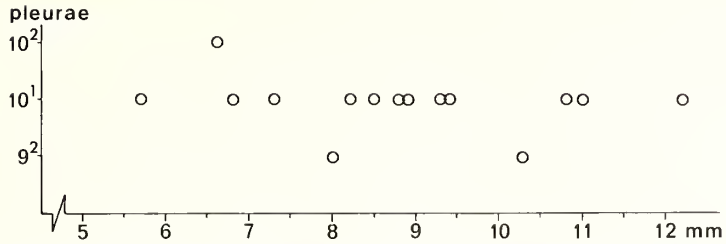
		9^1	9^2	10^1	10^2	11^1	11^2	12^1	$\bar{m}$	s	N
I	Form A total	—	5	12	9	9	2	1	10·42	0·62	38
II	Hemse Beds	—	—	5	8	7	2	1	10·69	0·54	23
III	Lau Backar 1	—	5	7	1	2	—	—	10·00	0·50	15
IV	Form B total	2	13	18	2	—	—	—	9·79	0·35	35
V	Hulte 3	—	2	12	1	—	—	—	9·97	0·23	15
VI	Mästermyr 1	—	8	3	1	—	—	—	9·75	0·45	12
VII	Form C	4	—	—	—	—	—	—	9·00	0·00	4

two types in Form B; one with very large eye and small field of cheek (Pl. 49, figs. 3 and 7), and one with smaller, taller eyes and relatively larger area of field of cheek (Pl. 40, fig. 2; Pl. 49, fig. 2). Form C is distinguished mainly by features in the posterior part of the pygidium, and may possibly be one end of the morphological variation within Form A (see Table 2).

Several species and subspecies with a morphology very close to *obtusus* have been described recently. Schrank (1972) erected *Encrinurus* (*Frammia*) *obtusus erraticus* for Ludlow specimens from German erratics (originating from the Baltic region). These specimens (regarded as a separate species by Tripp *et al.* 1977 and by following workers) fall well within the morphological range of the Gotland *obtusus* Form A material, and *erraticus* is treated here as a junior subjective synonym of *obtusus*. Specimens assignable to *obtusus* are also known from the Podolian Ludlow. The material, collected and kindly lent by Dr R. M. Owens, consists of about ten pygidia and two free cheeks from the Grinchuk Suite of the Malinovtsy Horizon, excursion localities 6 and 7 of Tsegelnyuk *et al.* (1983). Of seven pygidia there are five with 9^2 pleurae, and one each with 10^1 and 10^2 (compare with Mästermyr 1 in Table 2). The available material is indistinguishable from *obtusus* Form B. One similar pygidium is from the Sokol Suite, locality 5.

The British Ludlow specimens described by Tripp *et al.* (1977) as *E. rosensteinae* are more difficult to compare with the Gotland material. The holotype pygidium of *rosensteinae* has been studied and is slightly distorted, but very similar to *obtusus*, being somewhat intermediate between Form A and Form B, except for being more elongate, as are the other figured specimens apart from the complete exoskeleton (Tripp *et al.* 1977, pl. 115, figs. 1, 2, 7). This specimen, and other unfigured British material (e.g. BM I. 6197; see Tripp *et al.* 1977, p. 861), is similar to Gotland Form B specimens, and can be confidently assigned to *obtusus*. It is clear that the British material consists of two slightly different types. The only significant difference between *rosensteinae* (holotype and other elongate pygidia) and *obtusus* is the slightly higher R/P ratio in the former (confirmed in British material kindly loaned by Mr Stephen Tunnicliff, Nottingham). The possible synonymy of *rosensteinae* and *obtusus* can be confirmed only by further study of the British material.

E. dimitrovi Perry and Chatterton, 1979 (including *E.* (*Fragiscutum*) sp. of Perry and Chatterton 1977) from the Canadian upper Wenlock or lower Ludlow is even closer to *obtusus* than *rosensteinae*. Synonymizing of the two species here is only prevented by the difficulty in assigning the Canadian material to either one of Form A or Form B. Pygidia of *dimitrovi* have a pleural height intermediate



TEXT-FIG. 8. Number of pygidial pleurae plotted against pygidial length (articulating half-ring excluded) in *Balizoma obtusus* Form B. There is no correlation between size and number of pleurae. All specimens from Hulte 3 (Ar52337, Ar52423–52436).

between Form A and Form B, while cheeks and eyes are more similar to Form A. Canadian material similar to *obtusus*, from Avalanche Lake, is currently under study by Dr Brian Chatterton, Edmonton. The material seems to show weak dimorphism in the pygidium, with one form longer, higher and with slightly wider pleural furrows (Chatterton, pers. comm.). The only figured pygidium of *B. dakon* Šnajdr, 1983 from the Bohemian Ludlow is indistinguishable from Form A of *obtusus*, but no other parts have yet been figured, and the short description of *dakon* indicates that there may be differences in the cephalon. The Estonian Ludlow material mentioned by Nieszkowski (1859, p. 377), Schmidt (1859, p. 448; 1881, p. 224), Twenhofel (1916, p. 330), and Männil (1982*a*, p. 65) has not been figured, and the assignment to *obtusus* cannot be confirmed.

The American Wenlock *E. indianensis* Kindle and Breger, 1904 is remarkably similar to *obtusus* (photographs of the type material kindly supplied by Dr Philip Lane, Keele; specimen figured by Levi-Setti 1975 not conspecific). The cranidium has the same proportions, size and position of tubercles and lateral glabellar lobes, eye position and shape of the genal angle. The holotype pygidium has 11^1 pleurae, fifteen rachial rings and a sagittal groove with axial tubercles on most rings, and differs from *obtusus* only in the more elongate shape, resembling *rosensteinae*. However, there may be additional differences since *indianensis* is preserved as internal moulds, and the free cheek is unknown.

Differences between *B. variolaris* and *B. obtusus* were listed by Tripp *et al.* (1977, table 5), and although *obtusus* is interpreted in a wider sense here, the differences are obvious. *B. hyperboreus* (Thomas *in* Thomas and Narbonne 1979) has a pygidium similar to *obtusus* Form A, but is distinguished by a tuberculate 1L, denser glabellar tuberculation, and eyes set further from the rachial furrows.

REMARKS ON DISTRIBUTION

Upper Visby Beds. At Halls Huk 1 *E.* (*E.*) *punctatus* Form A occurs on the same bedding planes as *E.* (*E.*) *laevis* (Angelin, 1851; this species will be described separately elsewhere). The exact level of this co-occurrence is uncertain, but very close to the Upper Visby Beds/Högklint Beds boundary. The first appearance of *punctatus*, and the last of *laevis*, is therefore either in the top Upper Visby Beds or lowest Högklint Beds.

Högklint Beds. E. (*E.*) *punctatus* Form A is abundant in all units of this division.

Tofta Beds. No encrinurids have been collected in the Tofta Beds.

Slite Beds. From units a to e only poor material is known, apparently belonging to *E.* (*E.*) *punctatus*. In the oldest, northwestern area of the Slite marl, *E.* (*E.*) *punctatus* Form A makes its last appearance (Valve 2). In the remaining part of the Slite Marl *E.* (*E.*) *punctatus* Form C is abundant. *E.* (*E.*) sp. A occurs together with, but less commonly than, *E.* (*E.*) *punctatus* Form C in Slite Marl areas bordering to unit g (Follingbo 6, Hajdungs 1, Bolarve 1, Mojner 3). It is probable that *E.* (*E.*) sp. B

occurs slightly higher stratigraphically in the transition from Slite Marl to unit g. In the youngest, southwestern area of the Slite Marl, in the 'Pentamerus gothlandicus Beds', *E.* (*E.*) *punctatus* is replaced by *E.* (*E.*) *odvaldensis* (Odvalds 1, Svarvare 1, Robbjäns 1, 2).

Halla Beds. Poor material from unit b (Hörsne 5) seems to be close to *E.* (*E.*) *macrourus.*

Mulde Beds. E. (*E.*) *macrourus* makes its first appearance in the lower part (Blåhäll 1), and ranges through the division. In the uppermost Mulde Beds at Loggarve 2 *B. obtusus* occurs. This locality, on the edge of the Klinteberg Beds limestone area, may represent an environment similar to the near-reef Hemse Beds, where *B. obtusus* is present. The absence of *obtusus* in the Klinteberg Beds (and Mulde Beds) between Loggarve 2 and the Klinteberg Marl (Ajmunde 1) may thus simply reflect the absence of exposed near-reef strata in this area. No trilobites have been found in the southeastern area of the Mulde Beds.

Klinteberg Beds. Well-preserved trilobites are known only from Ajmunde 1 in the southwestern, marly part, originally mapped as Klinteberg limestone by Hede (1927); termed Klinteberg Marl by Laufeld (1974*a*). Jeppsson (1983) regarded this locality as belonging to the Hemse Marl NW on conodont evidence, a view supported by the trilobite distribution. At Ajmunde 1 *E.* (*E.*) cf. *intersitus* is abundant, and co-occurs with the less common *B. obtusus.*

Hemse Beds. This division consists of two, partly synchronous, main facies types; first, the northeastern outcrops of reefs and thick-bedded limestones; secondly, the more argillaceous, thin-bedded facies in the west and south (see text-fig. 9), divided into Hemse Marl NW and Hemse Marl SE. The faunal succession along the western coast is:

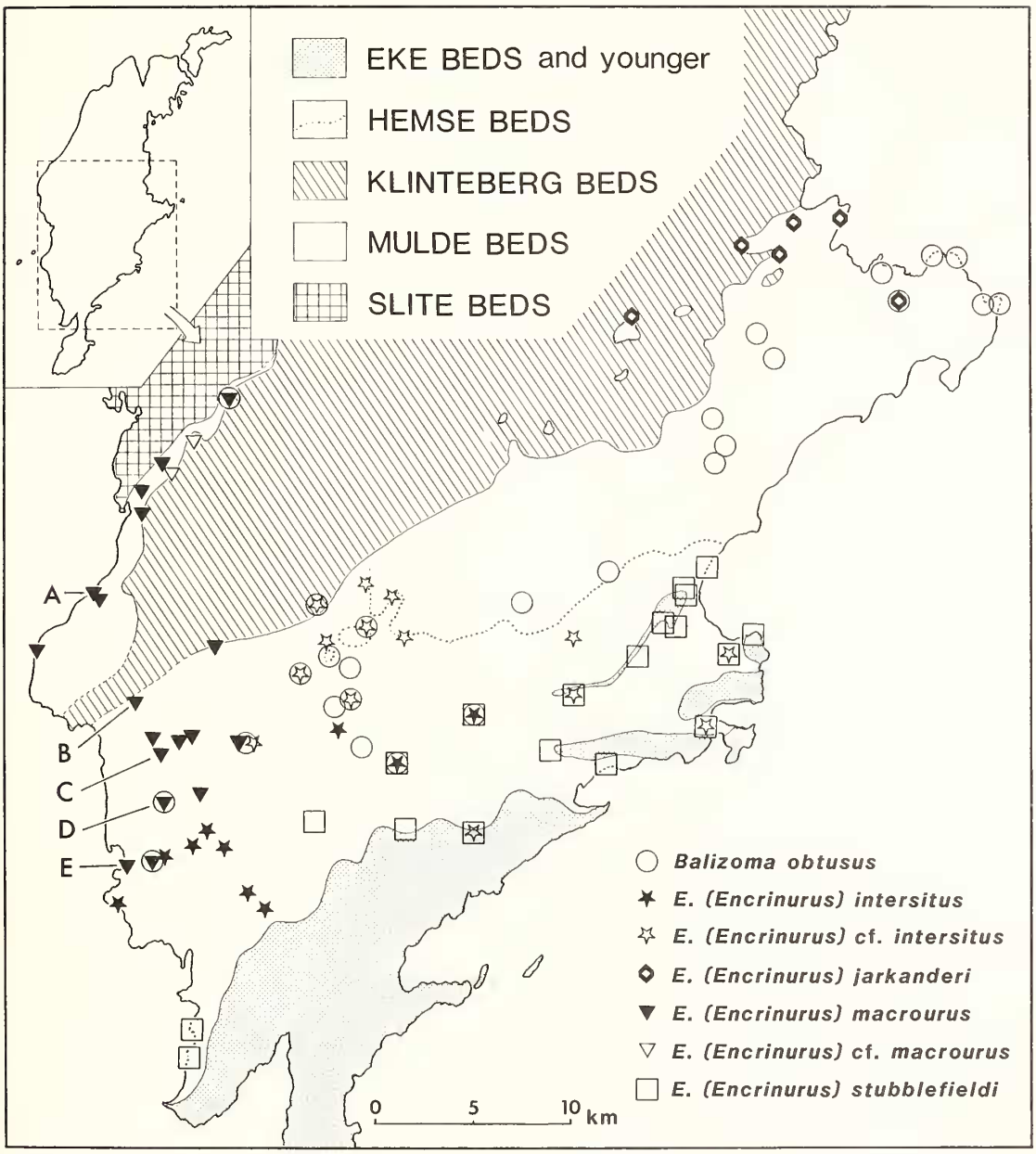
1. *E.* (*E.*) *macrourus* occurs north-west of a straight line approximately from Vakten (south of Petesvik) to Fardhem church. It co-occurs with *E.* (*E.*) sp. C at Urgude 3 and ?4.
2. Co-occurrence of *macrourus* and *B. obtusus* close to the above line (Lilla Hallvards 5, Smissarve 1, Mästermyr 1).
3. Replacement without overlap by *E.* (*E.*) *intersitus* (the possible co-occurrence of *macrourus* and *intersitus* at Mästermyr 1 is probably due to the relatively large sequence exposed, 2 or 3 m, which probably covers the level where the shift takes place).
4. Replacement by *E.* (*E.*) *stubblefieldi*, found at Klasård 1 and Vaktård 2. This occurrence agrees with the view of Jeppsson (1983, p. 133) that these localities represent a westerly continuation of the Hemse Marl SE. In the uppermost part of the Hemse Beds in this area, at Bodudd 1, encrinurids are apparently absent.

Inland of the above succession *E.* (*E.*) cf. *intersitus* co-occurs with *B. obtusus* in the Hemse Marl NW (Gardarve 1, Gerete 1, Amlings 1). *E.* (*E.*) cf. *intersitus* is also present in the strata immediately underlying the southwestern outcrops of the limestone area at Rangsarve 1, Ase 1, and Klints 1. According to Jeppsson (1983) at least the first of these localities should be referred to the Hemse Marl SE. The localities are situated at an elevation of 40 m and the southeasterly dip of the strata indicates an approximate time-equivalence with the more low-lying main area of the Hemse Marl SE.

In the main area of the Hemse Marl SE *E.* (*E.*) *stubblefieldi* is abundant until disappearing at, or slightly below, the Eke Beds boundary. It first co-occurs with *intersitus* and *B. obtusus* (Hulte 3, Västlaus 1) in ratios of about 3 : 3 : 1. Specimens referred to here as cf. *intersitus* co-occur with *stubblefieldi* at some localities in beds close to the Eke Beds boundary (within 1 or 2 m at most; Hägvide 3, Nyan 3, Öndarve 1, Sigdes kanal).

E. (*E.*) *jarkanderi* is restricted to unit b in the northernmost outcrops of the Hemse Beds. *B. obtusus* is characteristic of unit c of the limestone sequence. In the uppermost part of this sequence, unit e, specimens probably belonging to *E.* (*E.*) *nasutus* occur.

Eke Beds. Encrinurids are as yet only known from the Lau outlier. At Gannor 1 *E.* (*E.*) *nasutus* occurs both in the reefs and in layer *d* (of Hede in Munthe *et al.* 1925). The species continues into the upper Eke Beds at Lau Backar 1, where it is the commonest trilobite and co-occurs with *B. obtusus.* No encrinurids have been encountered in younger strata on Gotland.



TEXT-FIG. 9. Distribution of encrinurids in the Mulde, Klinteberg, and Hemse Beds. A–E indicate localities yielding the specimens with corresponding letters in text-figs. 5 and 6. The boundaries are those of Hede (1942).

Discussion. It is clear that the species have a markedly restricted vertical distribution, even more so when the different forms ('populations') are considered. This reflects either a restricted temporal span or facies dependence (the latter has been discussed extensively by e.g. Chlupáč 1977 and Lane 1972). The frequent horizontal and vertical facies changes in the Gotland sequence would strongly restrict the distribution of facies dependent species. When major facies changes are absent, as on the western coast from the lower Mulde Beds to well into the Hemse Beds, a series of populations forms a morphological cline through the sequence (*E.* (*E.*) *macrourus*). Such a cline makes the definition of the range of a particular species or chronosubspecies within the morphological series impossible or arbitrary.

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APPENDIX

Locality data

Locality names followed by numbers are defined according to the system of reference localities introduced by Laufeld (1974*b*) for Gotland, and are described in that study or in Larsson (1979), Jeppsson (1982), Cherns (1983), and Ramsköld (1983, 1984). Other localities are defined by twelve figure grid references according to the Swedish National Grid (Rikets Nät) system whenever possible. Nineteen new localities are described here.

HÄGSARVE 1, 634947 164391 (CJ 3048 4872), Sproge parish, *c.* 4150 m north-west of Silte church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Ditch exposure immediately south of the road junction. Hemse Beds, Hemse Marl NW.

HÄGSARVE 2, 634861 164415 (CJ 3066 4787), Sproge parish, *c.* 3400 m north-west of Silte church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Shallow ditch west of the road, running south-west from the road and along the side of the wood. Hägsarve 2 comprises the entire length of the ditch (*c.* 100 m). Hemse Beds, Hemse Marl NW.

HÄGSARVE 4, 634842 164430 (CJ 3080 4765), Sproge parish, *c.* 3200 m north-west of Silte church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Ditch exposure 0–50 m east of road/ditch intersection 900 m south-south-east of the west house at Hägsarve. Hemse Beds, Hemse Marl NW.

HULTE 3, 634725 165655 (CJ 4294 4557), Hemse parish, *c.* 1750 m south-east of Hemse church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Ditch section *c.* 150 m north-north-west of main road. Comprises from the corner of the ditch and 100 m toward south-west. Material excavated from the ditch is dumped 100 m south of the road at 634697 165651. Hemse Beds, Hemse Marl SE.

KAUPUNGS 3, 636358 167350 (CJ 6106 6054), Ardre parish, *c.* 1725 m south-south-west of Ardre church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 170 Katthammarsvik. Section immediately west of new road across Kaupungsklint, 0–100 m from junction with road to Ardre abandoned church ('ödekyrka'). Hemse Beds, units c and d.

KLINTS 1, 635622 165540 (CJ 4243 5457), Lojsta parish, *c.* 850 m south of Lojsta church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 164 Hemse. Temporary exposure during well construction at Klints. The excavated material is dumped 250 m north of Klints, at 635653 165537 (CJ 4245 5491). Hemse Beds, upper? part, and Hemse Marl SE?

LEVIDE 1, 635305 164753 (CJ 3440 5201), Levide parish, *c.* 940 m west-south-west of Levide church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 164 Hemse. Shallow ditch running north-north-west from the road, north of the road. The ditch is *c.* 30 m long. Levide 1 is located just north-east of the road junction. Hemse Beds, Hemse Marl NW.

LILLA HALLVARDS 5, 634202 164400 (CJ 3002 4131), Hablingbo parish, *c.* 4850 m west-south-west of Hablingbo church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Temporary exposure 5 m north of road, in excavation parallel to road, 400–600 m east-north-east of road junction at Lilla Hallvards. Hemse Beds, Hemse Marl NW.

LILLA HALLVARDS 6, 634221 164445 (CJ 3048 4146), Hablingbo parish, *c.* 4150 m west-south-west of Hablingbo church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Small exposure immediately south of the road to Lilla Hallvards in ditch perpendicular to road, in the small glade, *c.* 2500 m west-south-west of junction with main road. Hemse Beds, Hemse Marl NW.

LILLA HALLVARDS 7, 634278 164562 (CJ 3168 4194), Hablingbo parish, *c.* 2950 m west of Hablingbo church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Temporary exposure in pit for a metal post, immediately south of road to Lilla Hallvards, *c.* 1225 m west-south-west of junction with main road. Hemse Beds, Hemse Marl NW.

LUKSE 2, 634287 164745 (CJ 3354 4190), Hablingbo parish, *c.* 1100 m west of Hablingbo church. Topographical map sheet 5 I Hoburgen NO & 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Exposure in ditch running north-east to south-west, partly along the woods edge, 0–100 m from intersection with main ditch running south-east to north-west. Hemse Beds, Hemse Marl NW.

MÄSTERMYR 1, 634828 164873 (CJ 3520 4720), Silte parish, *c.* 2575 m north-east of Silte church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Drainage ditch section from the intersection of the smaller ditch from north-east, and 400 m toward south-east to the wooden bridge 475 m north-west of point 14.30. Hemse Beds, Hemse Marl NW.

MICKELS 1, 634590 164641 (CJ 3270 4501), Silte parish, *c.* 750 m south-west of Silte church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Exposure 5–25 m south of road in ditch running north–south, *c.* 250 m east of road junction at Hallvide. Hemse Beds, Hemse Marl NW.

ODVALDS 1, 636442 164518 (CJ 3291 6352), Klinte parish, *c.* 875 m west-north-west of Klinte church. Topographical map sheet 6 I Visby SO. Geological map sheet Aa 160 Klintehamn. Temporary exposure in excavation during construction of road running north-north-east from the main road *c.* 150 m west-south-west of the house at Odvalds north of the road. The excavation continued *c.* 100 m toward north-north-east and then 50 m west-north-west. Slite Beds, Slite Marl, 'Pentamerus gothlandicus Beds'.

ÖNDARVE 1, 634917 167234 (CJ 5877 4626), När parish, *c.* 3175 m south-east of När church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 156 Ronehamn. Low section in ditch running north-west to south-east along west side of road, 0–100 m from road/ditch intersection *c.* 1275 m east-south-east of the windmill at Frigges. Hemse Beds, top, and Eke Beds, base.

RUDVIER 1, 636260 167312 (CJ 6060 5960), Ardre parish, *c.* 2700 m south-south-west of Ardre church. Topographical map sheet 6 J Roma SV. Geological map sheet Aa 170 Katthammarsvik. Large quarry, marked on the topographical map, *c.* 200 m west of the main road where it passes Kaupungs. The boundary between the units c and d is exposed in the south wall of the quarry. Hemse Beds, units c and d. References: Mori 1970, loc. 116.

SMISSARVE 1, 634517 164437 (CJ 3065 4445), Silte parish, *c.* 2800 m west-south-west of Silte church. Topographical map sheet 5 I Hoburgen NO and 5J Hemse NV. Geological map sheet Aa 164 Hemse. The southeastern termination (at intersection between the wood and the field) of ditch running along, and south of, the road, 1600 m from the road junction at Siglajvs. Hemse Beds, Hemse Marl NW.

URGUDE 3, 635003 164375 (CJ 3038 4931), Sproge parish, *c.* 1425 m west of Sproge church. Topographical map sheets 6 I Visby SO and 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Exposure in ditch perpendicular to road, from road to main ditch running east-north-east to west-south-west 250 m north of road. Urgude 3 includes exposure in ditch on east side of road to Snoder, 0–200 m from junction with Sproge–Lindarve road. Hemse Beds, Hemse Marl NW.

URGUDE 4, 634996 164358 (CJ 3018 4925), Sproge parish, *c.* 1600 m west of Sproge church. Topographical map sheet 5 I Hoburgen NO and 5 J Hemse NV. Geological map sheet Aa 164 Hemse. Exposure in ditch perpendicular to road, 0–50 m south of road, along west side of small wood, *c.* 600 m east of the windmill at Kruse. Hemse Beds, Hemse Marl NW.

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